Quantifying the sociality of wild tool-using New Caledonian crows through an animal-borne technology

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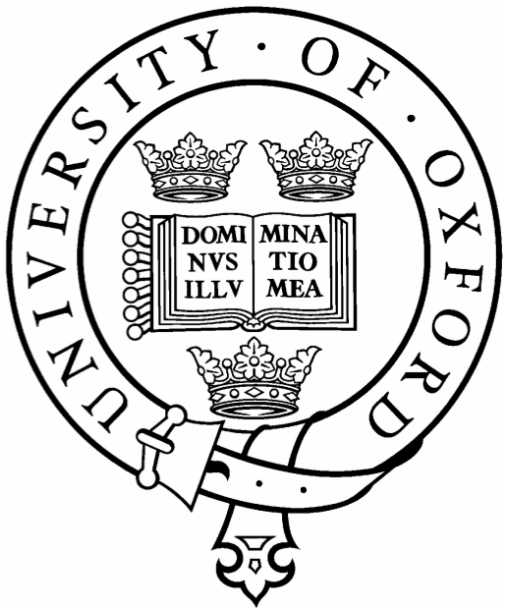

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Abstract

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New Caledonian crows (NC crows; *Corvus moneduloides*) are the most prolific avian tool-users and crafters, using up to three unique tool types derived from numerous plant materials. Since the discovery that wild populations of NC crows use and manufacture different tools in different locations with no measured environmental correlates to these distributions, the process by which NC crows acquire their tool-oriented behavior has been investigated. Two major findings were discovered in 2005: NC crows have a genetic predisposition to manipulate stick like objects, and they increase their rate of manipulation when exposed to social influences. Since then, much of the research into the sociality of wild NC crows has focused on direct social influences, especially the parent-juvenile relationship, yet no social network of wild NC crows has been described. In my thesis, I characterized a new proximity-logging device, *Encounternet*, and outline a four-step plan to assess error in animal borne devices; uncovered drivers, such as relatedness, space-use, and environmental factors, of wild NC crow sociality, and experimentally manipulated the social network, revealing immediate changes to the number of day-time and roosting partners, the breakdown of first-order relatedness driving sociality, and an increase in the amount of time NC crows associate; and revealed an indirect pathway via tools left behind by conspecifics allowing for the transmission of tool-properties between unrelated NC crows. Altogether, I furthered our understanding of wild NC crow sociality through the use of an animal-borne device, experimental manipulation in the wild measuring the response of the NC crow social network, and demonstrated the utility of animal-borne devices in mapping the network of a population of wild birds.

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Drew, I don't know how to thank you enough for helping me accomplish the final stages of my DPhil in New Caledonia—your friendship kept me sane and let me have just a little bit of fun while finishing the final experiment. All I have to say is that we definitely need to keep red-orange away from the logs!

While I was self-funded, I would like to thank Christian Rutz who supported my research activities through his BBSRC research grant, the Barbara Craig Fund at Somerville College to help me learn a little French, and the departmental fund for my amazing trip to Germany. To the people at Somerville, thank you for your assistance with housing during my last year. And to the Advanced Research Computing (ARC) facilities for support running my mixed model.

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And finally, Kevin—what can I say to thank you for everything you have done for me. You are the most amazing person I've ever met: here's to a future full of happiness and being able to take a deep breath when life requires it.

The way a crow
Shook down on me
The dust of snow
From a hemlock tree

Has given my heart
A change of mood
And saved some part
Of a day I had rued.

— Robert Frost

Author contribution statement

Regarding Zackory Burns' thesis submitted for the degree of Doctor of Philosophy in Hilary Term 2014 entitled, Q*uantifying the sociality of wild tool-using New Caledonian crows though an animal-borne technology*. All work contained herein is his own, except where noted below.

Chapter 1. Entirely his own work.

Chapter 2. Data was collected by Zackory Burns, Dr. Christian Rutz, Dr. James St Clair, Dr. Stephanie Ismar, Dr. John Burt, and Dr. Christiana Anagnostou. Physical model was derived by Dr. Richard James. Mixed models and simulations were completed in collaboration with Dr. Michael Morrissey. The first draft of this manuscript was written by Zackory Burns, with editing from all co-authors.

Chapter 3. Zackory Burns initiated this paper with Dr. Emiel van Loon, and wrote the first draft of the manuscript (except two paragraphs); Dr. van Loon edited the manuscript.

Chapters 4, 5, and 7. Dr. Christian Rutz initiated the idea to use *Encounternet* on wild New Caledonian crows, and funded the project through the BBSRC. Dr. John Burt, Dr. Brian Otis, and Jason Bowen built *Encounternet* at the University of Washington, USA. Zackory Burns, Dr. Christian Rutz, Dr. James St Clair, Dr. Stephanie Ismar, and Dr. Christiana Anagnostou deployed *Encounternet*, and all but Dr. Christiana Anagnostou collected data. Analyses were heavily discussed between Zackory Burns, Dr. Christian Rutz, Dr. James St Clair, Dr. Richard James, and Elaine Bettany; Zackory Burns performed all analyses presented here, except for the amalgamation of logs, which was performed by Elaine Bettany. Zackory Burns wrote all chapters.

Chapter 6. Data was collected by Zackory Burns, Drew Schaft, Barbara Klump, and Shoko Sugasawa. Video scoring was completed by Zackory Burns and Caitlin Higgott. Analyses were discussed between Zackory Burns, Dr. Christian Rutz, Dr. James St Clair, Barbara Klump, and Shoko Sugasawa. Zackory Burns performed all analyses, and wrote the first draft of the paper. All co-authors edited the manuscript.

Chapter 8. Entirely his own work, except for data collected as noted in chapters 4, 5, and 7.

Chapter 9. Zackory Burns initiated this paper with Kevin Liu, and wrote the first draft of the manuscript; Kevin Liu edited the manuscript.

Chapter 10. Entirely his own work.

Appendix 2. Experiment was devised and carried out by Antone Martinho and Zackory Burns in collaboration with guidance from Auguste von Bayern and Alex Kacelnik. Data collection and analysis were carried out primarily by Antone Martinho with assistance from Zackory Burns. Manuscript was written by Antone Martinho with input and guidance from Zackory Burns, Auguste von Bayern, and Alex Kacelnik. Permission to include as an appendix was given by Professor Adrian Thomas (DGS).

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CHAPTER 1

Animals interact with their environment and must forage to survive. Sometimes, as animals forage, they use external objects to facilitate their foraging. Yet, understanding the processes and conditions that facilitate the origin and maintenance of tool-use remains largely unknown. Conceptual advances, such as the dual inheritance theory (See Richardson and Boyd 2008; also known as gene-culture co-evolution) or niche construction (See Odling-Smee *et al*. 2003), have furthered research in three main fields of study: genes, environment, and sociality. Investigating these three concepts remains difficult due to the inability of directly observing the species, such as New Caledonian crows (*Corvus moneduloides*), exhibiting tool-use. Therefore, novel methodologies to investigate the interaction of these three, especially on wild animals, are necessary to further advance our understanding particularly on NC crows.

In this chapter, I describe the current state of knowledge about NC crows, discuss the historical observations of animal tool-use, and then outline a novel device that is attachable to animals to measure their behavior.

New Caledonian Crows

Tool-use has been documented in numerous species (Beck 1980; Shumaker, Walkup and Beck 2011) with a significant number studies of tool-use having been undertaken in orangutans (van Schaik *et al*. 2003), capuchin monkeys (*Cebus* spp.; Fragaszy *et al*. 2004), woodpecker finches (*Cactospiza pallida*; Tebbich *et al*. 2001, Tebbich *et al*. 2002), chimpanzees (Goodall 1964; Whiten *et al*. 1999; Whiten *et al*. 2005) and New Caledonian crows (Hunt 1996; hereafter NC Crows). Some populations of orangutans (van Schaik *et al*. 2003), capuchin monkeys (Fragaszy *et al*. 2004), and woodpecker finches (Tebbich *et al*. 2001, Tebbich *et al*. 2002) exhibit tool-use, while other

populations of these species do not exhibit tool use. In contrast, chimpanzees (Whiten *et al*. 1999) and NC crows (Hunt 1996; Hunt and Gray 2003) are believed to display population (or almost population) wide tool-use abilities; moreover, both species exhibit tool manufacture. This thesis will focus on the latter, NC crows, with this section focusing on the current understanding of NC crows' tool manufacture and use, morphology and ecology, cognition, and sociality.

Brief observations of NC crows using tools were described by Le Goupils (1928) and Orenstein (1972), reporting the use of stick tools to forage for hidden prey, which we now know to be beetle larvae (*Agrianome fairmairei*; Hunt 1996). In 1996, a paper published by Gavin Hunt (whom I was able to briefly meet during my time in New Caledonia), fundamentally changed our understanding of tool-use and manufacture in NC crows (Hunt 1996). In this paper, Hunt (1996) described two different types of tools, both being manufactured, that aided the extraction of hidden prey. As a consequence of this paper, intensive investigation into both captive and wild NC crows has been undertaken from numerous groups around the world (See references in Rutz and St Clair 2012).

Next, I discuss our current understanding of NC crows' tool manufacture and use, morphology and ecology, cognition, and social structure. A recent review written by Christian Rutz and James St Clair (Rutz and St Clair 2012; during the first year of my DPhil) extensively and exhaustively analyses most of these topics.

Tool use and manufacture

Currently, wild NC crows use three unique types of tools: non-hooked stick-tools, hooked stick-tools, and tools cut from Pandanus (*Pandanus spp.*) leaves (Hunt 1996; hereafter, 'Pandanus tools'). Stick-tools are generally collected from the environment

(Hunt 2000, Bluff *et al*. 2010; personal observation) and are composed of different materials, such as sticks, leaf petioles, grass stems, or fern stolons (Orenstein, 1972; Hunt 1996; Hunt 2008; Troscianko *et al*. 2008). Non-hooked stick-tools are used by NC crows to extract hidden beetle larvae in trees (Hunt 2000, Bluff *et al*. 2010, personal observation), though surprisingly little is known about the locations that wild NC crows use tools to extract prey (as stated in the review by Rutz and St Clair 2012).

To investigate whether tool-oriented behavior had a genetic predisposition, hand-reared NC crows were raised in one of two conditions: no social influences or human-demonstrated tool-use. NC crows raised in the non-social setting manipulated stick-like objects at the same time as the human-influenced crows (Kenward *et al*. 2005); yet, the crows raised in the human-influenced condition picked up and manipulated sticks more often than those in the non-social condition (Kenward *et al*. 2006), suggesting that social influences can alter tool-oriented behavior in NC crows. Altogether, these studies demonstrated that investigating tool-use in NC crows would require approaches from at least two factors: genetics and sociality.

Hooked-stick tools are manufactured by the selective removal of parts from a v-shaped twig, alongside 'sculpting' or crafting the hook-end (Hunt 1996; Hunt and Gray 2002; Hunt and Gray 2004; personal observation). Pandanus tools are manufactured from the leaves of the *Pandanus spp.* (screw-pine) tree, with different shapes being found in the counterparts, or the remains on the leaf after a tool was removed (Hunt 1996, Hunt and Gray 2003). Pandanus tools are manufactured through a series of rips and cuts (Hunt 1996, Hunt and Gray 2003). The leaves of the screw-pine tree contain sharp barbs alongside the outside of the leaves (Hunt 1996, Hunt and Gray 2003; personal observation). NC crows manufacture three unique shapes of Pandanus tools: narrow, wide, and stepped tools (Hunt 1996, Hunt and Gray 2003). Narrow tools are

manufactured through the removal of only the barbed edge portion of the leaf (Hunt 1996, Hunt and Gray 2003); wide tools include the barbed edge and a portion of the leaf, forming a long rectangle-like shape to the tool (Hunt 1996, Hunt and Gray 2003); and stepped tools include the barbs on the outside, with the inside of the leaf cut and ripped into steps (Hunt 1996, Hunt and Gray 2003).

An extensive survey has been undertaken to map tool shapes across the main island of Grande Terre, and a smaller island of Mare (Hunt and Gray 2003). Non-hooked and hooked stick tools have been observed in at least 11 sites (not including my personal observation with James St Clair of our core study population manufacturing and using hooked stick-tools; Hunt and Gray 2002). Pandanus leaves have been found at 21 sites (throughout both Grande Terre and Mare), revealing a unique distribution in the shape of the tools, as well as the number of steps present at each location (Hunt and Gray 2003). Some locations include only a single design, whereas other locations include all three designs: this geographic heterogeneity has led Hunt and Gray to suggest that it is possible that the tool-design is spread through social information exchange (Hunt and Gray 2003).

Morphology and Ecology

Two morphological features are unique to NC crows: their bill and binocular overlap (Troscianko *et al*. 2012). Troscianko *et al*. (2012) states that the straight bill combined with the largest binocular overlap amongst all measured passerine birds could be the first 'tool-use related morphological features outside of the hominin lineage'. It is possible that the straightness of their bill is due to selection from tool-use, or that their bill was unusually straight and thus acquired tool-use easier; unfortunately, we can only speculate on evolutionary drivers. Interestingly, Troscianko *et al*. (2012) approaches the

morphological adaptation considering tool-use to require binocular overlap to focus on the tip of the tool; it is possible that monocular selection necessitating cross-sagittal observation could have selected this large binocular overlap (See Appendix 2).

These unique morphological features facilitate wild NC crows to use and manufacture tools to acquire the necessary energy intake for survival. NC crows are opportunists, foraging on a wide range of food, including carrion, fruit, nuts, snails, adult and larval insects, and lizards (*c.f.* Rutz and St Clair 2012; Rutz *et* al. 2010). Wild NC crows have been observed using non-hooked stick tools to extract beetle larvae, using a tool to move leaf litter on the forest floor, and probing behind bark and into hollows (*c.f.* Rutz and St Clair 2012). Hooked stick tools have been observed doing all of the above, except it remains controversial as to whether hooked stick-tools are used for larvae 'fishing' (*c.f.* Rutz and St Clair 2012; personal observation). Contrarily, the use of Pandanus tools remains largely unknown, with only a few glimpses of wild foraging observed. Most of our knowledge stems from the Pandanus tools left behind by NC crows after use, suggesting the NC crows likely probe in the detritus of the screw-pine (*c.f.* Rutz and St Clair 2012, personal observation).

A novel approach to understand NC crows' evolutionary and ecological dependence on tool-use profiled the stable isotopes found in the feathers, blood and food to determine the link between energy intake and body upkeep (Rutz *et al*. 2010, note the correction: Rutz *et al*. 2011). This study determined that a significant amount of NC crows' intake—both proteins and lipids—came from beetle larvae that are obtained using tools (Rutz *et al*. 2010). Interestingly, this study determined that NC crows necessitate only a few larvae to reach their daily energetic intake for survival, thus revealing a high-energy reward for those successful in using tools to forage (Rutz

et al. 2010). Importantly, this study highlights the potential significance of tool-use in the evolution of this corvid species.

Cognition

The cognitive abilities of NC crows have been explored through numerous assays, advancing our understanding in the development and deployment of tool oriented behavior (*c.f.* Bluff *et al*. 2007). Much of the work has been with captive NC crows housed at Oxford University (under Professor Alex Kacelnik) and with temporarily housed NC crows captured in New Caledonia (under Dr Gavin Hunt, led by Alex Taylor). Specifically, I will describe spontaneous hook making (Weir *et al*. 2002), the trap-tube task (Kacelnik *et al*. 2006), and tool-choice and tool-use experiments (Chappell and Kacelnik 2002; Chappell and Kacelnik 2004); I will conclude with the limits to *understanding*.

Perhaps the best-known NC crow, Betty, was given a simple task: choose either the hooked wire tool or the straight wire tool to pull a bucket up a clear plastic tube using the bucket's handle (Weir 2005 Thesis). Unfortunately for Betty, her partner, Abel, removed the hooked wire tool, leaving Betty with a non-functional (non-hooked) tool for this task (Weir 2005 Thesis). However, this did not stop Betty from extracting the bucket, as she took the straight wire, pushed the tip of the wire into a depression in the duct-tape and bent a hook in the wire; she then managed to use this hook to pull up the bucket with food in it (Weir *et al*. 2002). From this, it is plausible that Betty's actions were 'to some extent goal directed' (Bluff *et al*. 2007), though as noted in Bluff *et al*. 2007, determining what the null hypothesis would be to test against limits our interpretation of Betty's actions.

The most widely used causal understanding test in physical cognition is the trap-tube task (Visalberghi and Limongelli 1994). The tube task is simple: a transparent horizontal tube is fitted with a 'trap' in the middle with food placed to one side of the trap, and the subjects are given a tool to retrieve the food from either end of the tube. In the fully functional position, the trap is faced downwards such that food could become trapped if pulled over the trap; in the non-functional position, the trap is facing upwards such that food cannot become trapped. Again, the only NC crow (known) tested to date is Betty: she failed to instantly solve the task, rather improving gradually over time (Kacelnik *et al*. 2006). Betty was able to pass the trap tube task after 110 trials, obtaining food on 8 trials out of 10 for three consecutive rounds of 10 trials. While it could be potentially interesting to compare Betty's performance to other animals, conclusions stemming from this comparison are limited because of our interpretation of the experimental design, such as the cognitive implications derived from not reverting to a 'random insertion' mode after the trap is removed (Bluff *et al*. 2007).

Another set of experiments were performed to determine NC crows' selection of tool properties, such as tool length, tool diameter, and possibly attending to the functional properties of their tools. Chappell and Kacelnik (2002) gave two captive NC crows ('Abel' and 'Betty') different length tools to extract food at different depths; both subjects selected tools that were long enough for the task, and selecting the longest tool more often than by chance. In addition, further work by Chappell and Kacelnik (2004) demonstrated that NC crows chose the thinnest diameter tool, when given a task necessitating a certain minimum diameter to retrieve a food reward. Similar work was undertaken to determine whether NC crows attended to the functional properties (hooks) of their tools. Altogether, Chappell and Kacelnik (2002, 2004) demonstrated that NC crows could preferentially select tools based upon their physical properties.

Holzhaider *et al*. (2008) experimentally tested wild-caught NC crows on wide tools, either facing the barbed edge in a functional position (barbs up) or in a non-functional position (barbs down); they revealed the crow would first use the tool as presented, rather than adjust the tool to the functional orientation. Unfortunately, it is possible that the presentation of the tool contained social information, and as such, the crow relied on social information rather than physical information of the tool. St Clair and Rutz (2013) published a similar study (of which I helped run trials) using hooked stick-tools, and demonstrated that wild-captured NC crows consistently adjusted the tool to use the hooked end, demonstrating they attend to the functional property of the hook.

Overall, NC crows have been shown to have interesting and, at times, surprising tool-oriented cognitive behavior. In addition to the above studies, other studies have revealed meta-tool use (Taylor *et al*. 2007), tool-use in series (Wimpenny *et al*. 2009), and context-dependent tool-use (Taylor *et al*. 2012). Corvid cognition has been of recent significant interest (Emery and Clayton 2004, Emery and Clayton 2005, Emery 2006) because of the plasticity in their behavior, and their ability to solve complex tasks. Future work exploring the cognition of these incredible tool-users, and other corvids, will (most likely) yield even more incredible advances to our understanding.

Sociality

Jenny Holzhaider, under the direction of Gavin Hunt and Russell Grey, provides much of our knowledge of wild NC crow sociality. In her dissertation (Holzhaider 2010), she qualitatively and quantitatively explored the social lives of wild NC crows, mostly through the use of feeding tables placed on a smaller outlying island, Maré; NC crows in Maré use and manufacture wide pandanus tools and non-hooked stick tools. Specifically, Holzhaider was able to quantify the home ranges of six males and social

structure of her population of NC crows (Holzhaider *et al*. 2011), and to qualitatively follow juvenile NC crows to discuss their potential to acquire information from conspecifics (Holzhaider *et al*. 2011, Hunt *et al*. 2012).

Numerous qualitative observations have been reported about NC crows' social activity. NC crows are generally observed, just after first light, foraging for beetle larvae in groups of 1-10 birds (Hunt 2000); on one occasion, a group of at least 30 birds were observed at a single location at a single time (Hunt 2000, personal observation). A core unit in the social lives of NC crows was observed to be a 'family unit' consisting of two adults and a juvenile identified through begging behavior (Hunt 2000, Kenward *et al.* 2004). Nesting was observed from October to January, agreeing with earlier work on wild NC crows in 1980 (Holzhaider *et al*. 2011 and Hannecart and Letocart 1980).

Holzhaider *et al*. (2010, 2011) and Hunt *et al*. (2012) quantified these qualitative observations to identify the core social structure of wild NC crows. Through the use of feeding tables, associations and behaviors were recorded, and these observations led to the suggestion that an adult male and an adult female form a social family that includes the current year's juvenile and, sometimes, the previous year's juvenile (Holzhaider *et al*. 2011). The pair-bonded adults appear to bond for multiple years, possibly for life, and after the death of their partner, they will pair bond with another adult (Holzhaider *et al*. 2011). The new adult tolerates the previous year's juvenile; though no observations of this adult provisioning the juvenile was observed (Holzhaider *et al*. 2011).

While much of the work has focused on identifying the core social unit, and observing interactions at localized food sources, no work has been undertaken to map the social network of NC crows, especially in an undisturbed, natural environment. In addition, understanding the mechanisms underlying associations will allow us to make

predictive models of information flow. Acquiring information about wild NC crows is challenging because the birds move away from observers in the field. Thus, to measure sociality, animal borne technologies must be used, and underlie the approach used in this thesis to measure and explore the social network of these fascinating wild birds.

Tool Use

Observations transform our understanding of the world, often leading to the rejection of long-held beliefs. In the study of animal tool-use, observations of Chimpanzees (*Pan troglodytes*) using tools in 1843 repudiated the claim that humans were the only tool-user (Savage and Wyman 1843-1844). Throughout the next *c.a.* 40 years, observations of tool-use in a variety of other species, including Indian elephants (*Elephas maximus indicus*), baboons (*Theropithecus gelada*), and orang-utans (*Pongo pygmaeus*), were documented (Darwin 1875). Synthesized in *The Descent of Man, and Selection in Relation to Sex*, Charles Darwin (1875) further rejected the notion that this behaviour was strictly an attribute of man. For over 120 years, the study of animal tool-use remained an eclectic record of brief observations until Jane Goodall transformed this in 1964 upon publishing the first quantitative study of tool-use in wild Chimpanzees at Gombe; the earnest study of animal tool-use finally commenced (Goodall 1964).

Sixteen years would pass, during which the publication of numerous studies (re-) defining tool-use occurred. In 1980, Benjamin Beck published the discipline's first book, *Animal Tool Behaviour*, cataloguing all observations of animals using tools. In this book, Beck synthesized across species by creating categories of tool-use defined by the actions of the tool; Beck referred to these categories as 'modes' of tool-use and placed each observation of tool-use into its respective group. The next 30 years of animal tool-use research has seen a sharp increase in the number of researchers and

research time dedicated to understanding the ultimate and proximate causes of tool-use in both the laboratory and in the wild. Following the first edition of *Animal Tool Behaviour*, a second edition of the book was published to provide an updated catalogue of animals that have been observed using tools. Synthesizing observations of tool-use included in the second edition (See Table 1) reveals that all currently defined modes of tool-use were observed before Goodall (1964).

Tracing the history of the study of animal tool-use reveals two fundamental shifts in thought: (1) humans were not the only tool-user (and in fact, tool-use was not confined to the closest extant species of man), and (2) a quantitative exploration of tool-use was possible. As more research effort has been devoted to the study of animal tool-use, we have witnessed an increasing amount of observations of new species using tools in the wild or laboratory, and the focus of animal tool-use shifting from simple observation to understanding the proximate and ultimate explanations of tool-use (*c.f.* Shumaker *et al*. 2011). In addition, we have begun to explore the necessary conditions that facilitate the origin and the maintenance of tool-use (*c.f.* Shumaker *et al*. 2011). It is at this point in time when my thesis enters the study of animal tool-use: I am interested in quantifying and synthesizing the role of sociality in the maintenance of tool-use in a wild population.

A note on the definition of tool-use

Throughout this thesis, tool-use will be defined as "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool" (Shumaker, Walkup and Beck

2011). While no definition of tool-use can capture exactly what it means to 'use a tool', this definition has become widespread in the field of animal tool-use because applying this definition separates a unique group of observations that have proven useful to advance our study of tool-use (*c.f.* Shumaker *et al*. 2011). This is not to say that a broader or more restrictive definition of tool-use wouldn't be useful (See Shumaker, Walkup and Beck 2011 for a review on the definition of tool-use).

Table 1: Observed modes of tool-use prior to Jane Goodall (1964). A mode of tool-use allows for a comparative analysis of tool-use across species; each mode is defined through the action of the animal with the object. The term provided in the column '**Mode of tool-use**' is from and defined in Shumaker, Walkup and Beck (2011). The primary citation for information stated in the column '**Example**' is bolded in the column '**Source**'.

Mode of tool-use	Example	Source
Drop	Orangutans broke off branches and spiny fruit of the Durian tree causing "a shower of missiles" that kept Wallace and others from approaching the tree.	**Darwin 1871**; Wallace 1869
Throw	Darwin had repeatedly observed chimpanzees throwing objects at people and records an observation of a baboon using mud as a projectile.	**Darwin 1871**
Drag, Roll, Kick, Slap, Push Over	Baboons in concert were observed rolling stones (some extremely large) down the side of a mountain at humans after being attacked.	Romanes 1892; **Darwin 1871**
Brandish, Wave, Shake	Boxer Crabs (*Lybia tesselata* and *Lybia edmondsoni*), detached small anemones from the substrate and waved one in each cheliped.	Bürger 1903; Duerden 1905; **Shumaker *et al*. 2011**
Bait, Entice	Male spiders of the genus *Pisaura* capture and present flies to females during courtship to avoid being eaten during copulation.	Bristowe 1929; **Shumaker *et al*. 2011**
Club, Beat	Darwin records observations of stones and sticks being used as weapons causing an orangutan to cover herself with either straw or a blanket.	**Darwin 1871**
Pound/Hammer	"The chimpanzee in a state of nature cracks a native fruit, somewhat like a walnut, with a stone".	**Darwin 1871**; Savage and Wyman 1843-1844)
Pry, Apply Leverage	Darwin witnessed a young orangutan place a stick into a crevice, and subsequently use the stick as a lever.	**Darwin 1871**
Dig	Captive Chimpanzees have been observed using sticks, pieces of wood, metal rods, nails, spoons, shovels and wire to dig in the ground.	Hayes and Hayes 1954; **Shumaker *et al*. 2011**
Jab, Stab, Penetrate	Captive chimpanzees have been observed jabbing conspecifics with sticks.	Köhler 1925; Sheak 1924; **Shumaker *et al*. 2011**
Reach	A captive orangutan used two sacks as a tool composite to reach an out of reach orange.	Yerkes and Yerkes 1929; **Shumaker *et al*. 2011**

Mode of tool-use	Example	Source
Insert and Probe	A captive orangutan used keys to open locks and padlocks.	Furness 1916; **Shumaker *et al*. 2011**
Scratch, Rub	Captive chimpanzees scratched or groomed themselves with sticks, straw or wood splints.	Köhler 1925; **Shumaker *et al*. 2011**
Cut	A captive chimpanzee was observed using scissors to cut her own hair.	Hayes and Hayes 1952; **Shumaker *et al*. 2011**
Block	Darwin witnessed a young orangutan cover itself with a blanket upon thinking that it would be hit.	**Darwin 1871**
Prop and Climb, Balance and Climb, Bridge, Reposition	A captive chimpanzee climbed and balanced on a pole to reach a suspended food reward.	Köhler 1917; **Shumaker *et al*. 2011**
Hang	A captive orangutan twisted straw into a rope and hung the rope over a bar in the cage and swung on the rope.	Hornaday 1922; **Shumaker *et al*. 2011**
Contain	Captive gorillas used hollow objects or their food boxes to hold drinking water.	Carpenter 1937; **Shumaker *et al*. 2011**
Absorb	A wild male gila woodpecker detached pieces of bark and soaked them in a honey solution, and transported the honey-soaked bark to his nestlings.	Antevs 1948; **Shumaker *et al*. 2011**
Wipe	Wild chimpanzees were observed pressing grass and leaves to bleeding wounds.	Savage and Wyman 1843; **Shumaker *et al*. 2011**
Affix, Apply, Drape	Captive elephants placed hay and grass over their backs.	Furniss 1879; **Shumaker *et al*. 2011**
Symbolize	Captive, encultured chimpanzees have been observed carrying toys or dolls in some manner.	Hayes 1951; **Shumaker *et al*. 2011**

Animal-borne technologies

History and devices

Stemming from our curiosity to understand animals in their natural environments, the field of animal-borne technologies, or devices attached to animals that measure some aspect of their lives, was born. Beginning in the late 1950s and early 1960s, two plenary studies established the field of animal biotelemetry through the use of a transmitting animal-mounted device that could be received by an observer (Le Munyan *et al*. 1959 and Eliassen 1960): Le Munyan *et al*. (1959) implanted a transmitter to monitor chipmunk heart rates, and Eliassen (1960) placed an externally-mounted transmitter to monitor the heart and wing beats of a mallard duck (*Anas platyrhynchos*). Although these first tags lacked complexity, transmitting a continuous stream of signal to be recorded, these studies established the use of transmitting radio signals to record parameters from the tagged-animal. During the following two decades, these transmitting tags were used to record the locations of animals—revealing the ability to track individuals over time—a key constraint for many species that cannot be uniquely identified in the wild (Cochran and Lord 1963, Marshall and Kupa 1963). The ability to track individual animals has led to the quantification of behavior and associations, and to numerous manuals to address the technical and methodological limitations of radio-tracking (for a review on basic equipment, see Kenward 1987; for a comprehensive historical review, see Kenward 2001).

In the beginning, animal-borne devices were not differentiated based upon the data collected from the individual, since using radio waves to track an individual or acquiring physiological measurements in real-time were significant advancements (*c.f.* Kenward 2001). Yet, since technologies have advanced considerably from the original tags, three primary types of data are collected from a variety of devices (and these are

not always independent of one another): behavior (actions), physiological measurements, and movement patterns. For example, video cameras have been used to observe animals in their natural environment, revealing never before observed behavior, such as the discovery of a novel material (grass stem) used as a tool (Rutz *et al*. 2007, Troscianko *et al*. 2008). A need to understand physiological measurements drove the initial tags, with radio waves transmitting heart rates (Cochran and Lord 1963, Marshall and Kupa 1963) and more recent studies focusing on the energetic costs associated with conservation (Wikelski and Cooke 2006), daily energetic necessities for survival (Steiger *et al*. 2009), and energetic rates during soaring and migration (Sapir *et al*. 2010). Movement animal-borne technologies have been driven by the need for better batteries, higher resolution data, and the ability to make devices lighter to be deployed on smaller animals (*c.f.* Rutz and Hays 2009). Since this thesis focuses on the movement of wild birds, the next section will explore movement animal-borne technologies.

Animal-borne technologies measuring movement

Numerous methods have been developed to measure the movements of animals, including GPS devices, RFID/PIT tags, acoustic loggers, and proximity devices (for reviews, see Rutz and Hays 2009, Hebblewhite *et al*. 2010, Cagnacci *et al*. 2010, Tomkiewicz *et al.* 2010, Krause *et al*. 2011). In addition, the medium in which the animals are moving, either terrestrial or aquatic, has driven the development of different technologies to suit the environment (Rutz and Hays 2009, Krause *et al*. 2013). While characterizing aquatic animals has triggered a huge advancement in acoustic loggers, or the ability to use sound to identify location, I will focus on terrestrial devices since this thesis focuses on terrestrial animals.

With the advent of satellites capable of triangulating devices on the surface of the Earth in 1973, the use of GPS for numerous biological questions has grown substantially (Hebblewhite *et al*. 2010, Cagnacci *et al*. 2010, Tomkiewicz *et al.* 2010, Krause *et al*. 2011). GPS devices have been deployed on numerous taxa (*c.f.* Rutz and Hays 2009, Hebblewhite *et al*. 2010, Cagnacci *et al*. 2010, Tomkiewicz *et al.* 2010, Krause *et al*. 2011), though they remain too heavy to be deployed for sufficient duration on small animals, such as passerine birds (Krause *et al*. 2011). Overall, GPS devices have enabled collection of home ranges, dispersal, population dynamics, and resource use of numerous large animals (Hebblewhite *et al*. 2010).

RFID/PIT tags, or passive transponders read by static receiver stations, were deployed subsequently as a system requiring no animal-borne battery, allowing for lengthy deployments on small taxa, such as passerine birds and bees (Psorakis *et al*. 2012, Aplin *et al*. 2012). Unfortunately, RFID/PIT tags have very short reading distances (usually less than 1 meter), and can have a high rate of missed detections (Krause *et al*. 2011). Moreover, RFID/PIT tags can only be read at receiver stations, thus no sociality patterns can be determined away from these receivers (Psorakis *et al*. 2012). While RFID/PIT tags have many deployment advantages, mapping the social network anywhere in the environment is essential to minimize error and maximize biological outcomes, such as mapping information or disease transmission through a network.

Altogether, the field of animal-borne devices has lacked a user-friendly system that is capable of direct transmission of signals between tags—necessitating only a single datum to determine association patterns (Krause *et al*. 2011). Next, I describe the history of proximity devices, and then discuss briefly the limitations a new device, *Encounternet*, overcomes.

Proximity devices

Four proximity devices have been independently developed, with each improving on its predecessor due to increasingly miniaturized components (Krause *et al*. 2011): *MateID* (Ji *et al* 1999 and Douglas *et al* 2006), *ZebraNet* (Juang *et al* 2002, Zhang *et al*. 2005), *encounter* (Prange *et al*. 2006), and *EcoLocate* (Markham and Wilkinson 2008). Proximity devices transmit radio waves between animal-borne tags, creating a single log for each encounter, or when two tags come within a certain distance of each other.

The first two developments of proximity devices, MateID and ZebraNet, were to be deployed on wild animals to monitor their movement, and although limited in scope, both deployments demonstrated proof of principle, though, on captive (MateID) and wild (ZebraNet) animals. MateID tracked possums (*Trichosurus vulpecular*) in a cage to a feeder, revealing a *ca.* 99% success rate identifying when the possum interacted with the feeder; however, this was not true when two or more possums interacted within 40 cm of a feeder (Douglas *et al*. 2006). ZebraNet was deployed on wild plains zebras (*Equus quagga*) to track their migration patterns and local scale movements (Juang *et al*. 2002). Unfortunately, ZebraNet failed as a consequence of a previously unknown constraint: the animals were far too mobile for sufficient data to be collected to quantify association or space-use patterns (Zhang *et al*. 2005).

In 2006, a new system, *encounter*, was developed and had much more success capturing associations between individuals (Prange *et al*. 2006). Prange *et al*. (2006) fitted 42 free-ranging raccoons (*Procyon lotor*) and tracked their associations, successfully downloading logs from 35 individuals. Furthermore, confirmation of association time was undertaken, and the tags were accurate to within 3 seconds for short durations (less than 300seconds) and by less than 30 seconds with encounters lasting between 8 and 14 hours (Prange *et al*. 2006). In 2008, another proximity device

was developed, named *EcoLocate* (Markham and Wilkinson 2008), though this device has remained as a prototype.

Unfortunately, all of these devices were intended for large animals and do not meet the ethically accepted percent of body weight for deployment on small animals (between 3-5%; Rutz and Hays 2009); though half of nearly 300 studies used devices greater than 5%, a sure sign that ethical obligations are not fully considered in the field (O'Mara *et al*. in press). A new technology was developed, and is used as a core part of this thesis named *Encounternet*, and a recent TREE review discusses this technology as the breakthrough necessary to map associations and space use in small animals (Krause *et al*. 2011). In my thesis, I describe *Encounternet* and discuss the successes (and failures) of this newly developed system in its first deployment.

Overview of Thesis

Overall, the aim of my thesis is to quantify the sociality of wild New Caledonian crows through the use of a novel animal-borne technology (*Encounternet*) and experimental manipulations in the field. Specifically, I sought to further our understanding through:

1. Exploring and quantifying the properties of *Encounternet*'s primary device: The animal-borne tag (Chapter 2);
2. Expanding the process from aim 1, to establish a framework to explore error in animal-borne technologies (Chapter 3);
3. Assessing the data from *Encounternet* to reveal basic network properties (Chapter 4);
4. Quantifying changes to the network in response to an experimental manipulation in the wild (Chapter 5);

5. Determining whether NC crows preferentially re-use tools left behind by conspecifics (Chapter 6);
6. Quantifying wild NC crow home ranges, and determine the potential to encounter another wild NC crow's abandoned tool (Chapter 7);
7. Exploring an alternative method to filter data from proximity devices (Chapter 8); and
8. Discussing the role of animal-borne technologies in developing policy (Chapter 9).

Altogether, the aim of my thesis is to both understand the role of animal-borne technologies to collect and quantify data, and to use the deployment of a novel device to quantify the sociality of wild tool-using New Caledonian crows.

There are two main sections in this thesis: (1) Methods, (2) Empirical Experiments. Following these two sections, I discuss the role of animal-borne devices to inform public policy and synthesize the contribution of my methodological and empirical work.

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Section 1: Methods

Introduction to Section 1

This section contains analyses to inform and improve our understanding of error in animal-borne devices. In Chapter 2, we explore the necessary steps to validate and calibrate *Encounternet*, a novel animal-borne proximity device. Therein, we aim to develop a physical model of radio-wave propagation, convert this physical model into a statistical model parameterized by data collected *in situ*, and calculate the probability that a property recorded in the field (power) matches a given distance (meters). Altogether, we use the output from this chapter to inform the biological outcomes explored in Section 2, and reveal that for each recorded power, a range of distances could be assigned to this value.

In Chapter 3, we outline a framework to calculate error in animal-borne devices through four simple steps: *know, identify, evaluate,* and *store*. We identify three processes by which error is introduced into animal-borne devices, and construct a framework to explore similar processes regardless of technology deployed. Overall, we seek to ensure that the method used limits the biological conclusions drawn.

CHAPTER 2

CALIBRATING ANIMAL-BORNE PROXIMITY DEVICES: CONVERTING RECEIVED POWER INTO DISTANCE (TABLE OF CONTENTS) 34

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Calibrating animal-borne proximity devices: Converting received power into distance

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Running title: Distance derived from received power

Keywords: animal social networks, biologging, *Corvus moneduloides*,

Encounternet, received signal strength indicator (RSSI), sociality

Summary

1. Studies of social networks measure the proximity and/or interactions between individuals. An increasingly common method in the wild is the deployment of technologies, such as GPS or proximity devices.
2. Proximity devices rely on the ability to detect another tag's signal, and to record the unique ID, the time and date of the encounter, and the power of the received signal after standardizing the value (named a *received signal strength indicator* (RSSI) and measured in decibels). While all current deployments of proximity tags rely on this RSSI value to characterize the distance between two tags, there is no standardized protocol to convert RSSI to distance.
3. We developed a step-by-step process to convert RSSI to distance by calibrating the environment in which the proximity tags will be deployed to quantify the attenuation of RSSI due to extrinsic factors, such as tag height, habitat, and relative antenna orientation. In addition, we quantified attenuation due to tag performance or the variation between individual tags in transmitted signal strength.
4. We derived an ideal theoretical relationship between RSSI and distance from basic physical properties, and then, to account for the non-ideal nature of the real environment, we applied this theoretical relationship to inform our generalized linear mixed model (MCMCglmm) to quantify the effects of height, habitat, relative antenna orientation, and the power of tag transmission. Altogether, we estimated the mean relationship between RSSI and distance, and importantly, determined confidence intervals on our estimates of distance from RSSI.
5. Because tags deployed on wild animals record RSSI values, we developed a simulation defined by the statistical parameters derived from our GLMM model to quantify the unique probability of each distance per RSSI. We optimized our

predictive power by weighting our simulations such that they are representative of our subjects' use of both habitats and heights, revealing a more refined distance estimate.

6. Our analyses demonstrated that a calibration exercise to convert RSSI to distance is essential, and further, the importance of performing the calibration at the actual site in which the study will take place to determine more accurately attenuation effects by taking into account movement patterns, morphology, and behavior of the study species. To facilitate future calibration exercises, we presented a checklist to aid quantification of signal attenuation for each deployment of proximity devices.

Introduction

Measuring who associates with whom is necessary to map social networks of animals. Yet, quantifying sociality in wild animals is a major challenge for biologists, especially when animals avoid, or the environment impedes, direct observation. To overcome this obstacle, animal-based technologies have been developed to record associations autonomously (for reference see Cooke *et al.* 2004; Rutz & Hays 2009; Krause *et al.* 2013). Proximity devices, which directly exchange uniquely identifiable and time-stamped radio pulses between animal-mounted tags, have been used to quantify patterns of inter-and intra-specific association (Böhm *et al.* 2009), to reveal predator-prey dynamics (Tambling & Belton 2009), and to identify pathways for disease transmission (Ji *et al.* 2005; Böhm *et al.* 2008; Hamede *et al.* 2009). Recent technological innovations have made proximity devices small enough to deploy on passerine birds, and increased the capacity of these devices to record a larger range of maximum distances between two tags, and to log encounters at a high enough resolution to observe real-time movement and association patterns (Rutz *et al.* 2012).

While these improvements to proximity devices will allow deployment on an increasing number of taxa, no standardized method has been established to convert the power of the received signal (known as the *received signal strength indicator*, or RSSI), into the actual distance between two tags. Previous studies have measured the maximum distance over which a certain RSSI value might be received (Böhm *et al.* 2009; Hamede *et al.* 2009), quantified intra-tag variation (Drewe *et al.* 2012; Boyland *et al.* 2013), and developed *post hoc* methods to correct for between-tag variation in transmission power (Boyland *et al.* 2013); yet, none of these studies integrates these findings into a comprehensive model. Currently, there are two programmable methods to deploy proximity devices to record RSSI values, and thus muddle our estimation of distance: (1) *a priori* programming of the device to record pulses if, and only if, a certain RSSI value is reached (e.g., *enCounter*; Prange *et al.* 2006); and (2) *post-hoc* filtering of data by RSSI value after having recorded the RSSI value of every received pulse (e.g., *Encounternet*; Rutz *et al.* 2012). While these two methods differ in functionality, the same underlying principle is used: an RSSI value must be converted to distance while taking into account variation attributable to environmental factors (such as habitat structure) and/or behavior of the animal. Since this principle is uniquely addressed for each deployment of a proximity device, a standardized method to convert RSSI to distance would ensure that the resolution of the technology in determining distance moderates biological conclusions.

Here, we present an approach to convert RSSI to distance for proximity devices. First, we systematically collected data on factors that could contribute to altering the signal strength, such as the height off the ground, within the environment of the prospective deployment. Then, we applied a four step process to convert RSSI to distance by: (1) developing a model derived from basic physical principles

establishing a theoretical RSSI-to-distance relationship; (2) parameterizing the model with empirical data to understand the mean fit of this relationship relative to experimentally assessed factors; (3) applying a mixed-effects model to our data to estimate the error of our predictive fit, and variation in tag performance; and (4) simulating RSSI values that could be assigned to a certain distance based on statistical parameters from our empirical data. Finally, we developed a step-by-step checklist to aid biologists in calibrating their respective deployments of proximity devices on other animals. Altogether, we aim to calibrate the *Encounternet* system to determine which received power we expect to correspond to a specified distance, and to establish a calibration methodology for future work to utilize.

Proximity logging system

We used a proximity logging system, *Encounternet*, that consists of three components: (1) animal-mounted tags that transmit, receive, and store coded radio-pulses; (2) stationary transmitting, receiving, and logging stations (base stations); and (3) a custom Yagi antenna, or a metal device that captures signals transmitted in the environment, mounted with a wireless transmitter and receiver for communication with all other components (master node; for a complete description of the system deployed, see the main text and supplementary online figure 1 in Rutz *et al.* 2012). Tags send 'ID' encoded radio pulses at a programmable time interval, and also receive and store 'ID' pulses (logs) from other tags. After the on-board memory of each tag surpasses a programmed level uniquely specified for each base station, the base station requests the recorded logs from each tag; after successful transfer of logs, the base station sends a command to remove the logs from tag memory. Additionally, each base station records pulses transmitted by the tags. The 'master node'

communicates with tags and base stations to download logs, or to check and reprogram parameters, if desired, amongst other functions (see supplementary online material in Rutz *et al.* 2012). The master node communicates only when a user triggers the initiation of a communication event (*e.g.*, the user would transmit a signal to check the time on a tag, and the tag would respond with the time to the master node).

Data collection in the field

We developed a method to collect RSSI values at specific distances, and to resemble the placement of tags on New Caledonian crows (NC crow; *Corvus moneduloides*). To measure the range of possible RSSI values per distance, proximity tags were (1) positioned in the same location and orientation that would be used in the deployment on NC crows (Rutz *et al.* 2012), (2) mounted in a grid that allowed multiple distances and relative antenna orientations (see Figure 1a), and (3) placed in five habitats at two heights.

To resemble NC crow bodies, store-purchased, plucked quails (*Coturnix japonica*) were used. Because the purchased quails lacked internal organs, chicken (*Gallus gallus*) livers were stuffed into their body cavities until full. The quails were placed inside rubber balloons before weighing (see Figure 1b), as a precaution to avoid mass loss due to water evaporation. A tag was then mounted on the mid-section of the dorsal surface of each quail, with the tag's antenna running along the spinal column towards the tail.

After packaging, the quail-mounted radio tag was positioned in one of three places (0 cm, 0.93 cm and 1.90 cm) along a 2-cm diameter plastic (PVC) pole (see Figure 1c). Tags were consistently mounted at 45° from the vertical, approximating

the tag orientation of a standing or perched NC crow. On each pole, the quail (with tag) was placed in one of three positions (*i.e.*, rotated in the horizontal plane) to measure possible (and extreme) tag-to-tag orientations; individual tags were randomly assigned a new location on a pole each day, and tags that were non-functional at the start of a trial were replaced.

Each pole, with the 3 quails attached, was then placed in parallel to all other poles at specified distances (see Figure 1a, d and e). For the first day of our trials, we placed 12 tags on 4 poles, and for the second and third days, we placed 18 tags on 6 poles. On day one, the poles were placed along a transect at 0, 4, 13 and 25 meters, and on days two and three, the poles were placed at 0, 1, 4, 7.5, 13 and 25 meters (see Figure 1a). Poles were randomly assigned to a distance at each location.

Twenty-four trials, or the period of time during which tags pulsed every 20 seconds, lasting 15 minutes each were carried out in five habitats. Locations were chosen to represent the primary vegetation of the study area, as well as to measure the variation within each habitat type. Habitats were designated by their primary component, and were subsequently denoted as: Casuarina (*Casuarina sp.*), Ficus (*Ficus sp.*), gallery forest (primarily tall 'candle-nut', *Aleurites moluccana*, trees with sparse or non-existent understory), Melaleuca (*Melaleuca sp.*), and shrubby (dense undergrowth). Two heights (0 m and 4 m above the ground) were sampled at each location, and were designed to represent crows on the ground, and, within methodological limitations, crows in the canopy.

Model derivation

To quantify RSSI values received at each distance, we derived from basic physical principles a model to describe the propagation of radio waves between two tags at

some distance from one another, designated by r and measured in meters. We assumed that as a signal propagates through space (treated as a homogeneous, isotropic medium), the waves undergo spherical spreading, and exponential decay due to scattering and/or absorption. The power, P_r, received by a tag, relative to a standardized reference power, P_0, is defined as:

$$P_r/P_0 = C(10^{-\beta r/10)} / r^2) \qquad \textbf{Equation 1}$$

The absorption coefficient β (≥ 0) is a function of habitat and height. For model derivation, the multiplicative factor, C, is a function of a tag's transmitting power, receiving ability, and tag/antenna orientations (all described below). The expected RSSI value recorded, in decibels, is

$$RSSI = 10\log_{10}(P_r / P_0) = \kappa - \beta - 20\log_{10} r, \qquad \textbf{Equation 2}$$

with $\kappa = 10\log_{10} C$. Larger values of β represents more rapid decay of RSSI; factors altering κ will change the intercept. Additionally, for any combination of κ and β, the slope of the curve is greatest at small inter-tag distances (r).

Variable tag power

Tag power influences κ, implying that any variability between tags in transmitted power will affect the recorded RSSI. Evidence from another deployment using similar technology (*Encounternet* without tag-to-tag communication) suggests that there are significant differences between tags (Mennill *et al.* 2012). While many tags were used in the calibration exercise, the variability in tag power was not recorded explicitly.

Instead, we quantitatively evaluated each tag's ability to transmit and receive pulses (see *fixed effects* below).

Tag orientation

Another factor influencing κ, the intercept in our model, is the relative pairwise tag orientation. Since the tags deployed in the calibration dataset had whip-antennae, we assumed that each bird-mounted antenna acts as a perfect dipole with the classic doughnut-shaped antenna pattern described by the function $\sin^2\alpha$, where α is the angle measured from a line along the antenna. We assumed that this pattern is unaffected by the closeness of the bird on which it is mounted, except that the bird acts as 'ground plane' to turn the inherent monopole structure of the antenna pattern into a dipole. In each calibration measurement, all tags were at the same height and were mounted at 45° to the vertical. A toric section, or the intersection of a plane at 45° to the $\sin^2\alpha$ doughnut, describes the in-plane radiation pattern for a single tag. Mathematically, this section is described by $\cos\alpha = \sin\theta/\sqrt{2}$, where θ is the angle shown in Figure 2a. Rearranging, the in-plane radiation pattern is $I(\theta) = \frac{1}{2}(1+\cos^2\theta)$. Twice as much power radiates to the sides as to the front and back (see Figure 2b). Note that doubling power corresponds to adding *ca.* 3 decibels to a RSSI measurement.

The receiving tag antenna has an identical in-plane radiation pattern, tilted at an angle ϕ to the line-of-sight from one tag to another. The directivity pattern $D(\theta,\phi)$ determines the attenuation effect on the received power, P_r, due to the relative orientation of the transmitting and receiving tag, and is defined as the product of two tag radiation patterns: $D(\theta,\phi) = \frac{1}{4}(1+\cos^2\theta)(1+\sin^2\phi)$. Thus, the attenuation effect, notated as δ, on an RSSI signal is $\delta(\theta,\phi) = 10\log_{10}D(\theta,\phi)$, which has a maximum of 0 decibels when tags are side by side (*e.g.*, θ=0°, ϕ= 90°), a minimum of *ca.* -6 decibels

when tags are aligned parallel (*e.g.*, θ=90°, ϕ= 0°) or anti-parallel (*e.g.*, θ=90°, ϕ= 180°), and an average value, taken over all possible combinations of relative orientation, of -2.75 decibels. We adapted our derived equation above to include δ; thus, our final theoretical equation to describe the relationship between RSSI and distance is:

$$RSSI = \kappa - \beta r - 20\log_{10} r + \delta + \varepsilon \qquad \textbf{Equation 3}$$

Development of mixed-effect model using the derived physical model

To quantify the statistical variation attributed to specific factors from the data collected *in situ*, we developed a generalized linear mixed-effects model (MCMCglmm; see Hadfield 2010) using R (R Development Core Team 2013). The fixed effects in our model included distance, height, habitat, and relative antenna orientation; we used the physical model described above to define the 'perfect world' rate of radio wave attenuation traveling in space. Random effects were built into our model to control for a tag's power at transmission, a tag's ability to receive a pulse, and an experimental design limitation with tags not being randomized between trials (*i.e.*, three tags were mounted on the same pole, and did not get randomized to one another each day), and were included as measured values from our *in situ* data collection. The optimum transmitting and receiving ability of all tags and the attenuation effect due to our fixed effects determined the intercept and the slope, respectively.

Thus, we defined our mixed effect model as:

$$RSSI_{ijklmno} = \kappa - \beta_{jk} r_i - 20\log_{10} r_i + \eta\delta_n + b_l^{send} + b_l^{receive} + b_l^{samepole} + \varepsilon_i$$

Equation 4

Subscripts were defined as: (*i*) individual datum, (*j*) habitat, (*k*) height, (*l*) sending tag, (*m*) receiving tag, (*n*) 'samepole'; samepole was defined as a set of tags that were assigned to the same pole to be randomized each day. We placed a coefficient, η, in front of δ, to allow the model to optimize the correction of power due to relative antenna orientation differences; we describe the significance of η below. A general coefficient, *b*, was used before each random factor, characterized in the superscript and subscript.

We used default diffuse normal priors on fixed effects, and flat priors on the variances of the random effects. Convergence was checked by calculating the effective number of samples, and by observing the traces of the posterior distributions of each parameter.

Fixed effects

To determine whether the variation in our data is homoscedastic, we compared σ for all height and habitat combinations. Table 1 presents β (slope) and σ (error) of our fits for unique height and habitat combinations. We qualitatively concluded that our data is homoscedastic across our measured distances. The MCMCglmm fit for each unique height and habitat combination, and a cumulative fit of all data is presented in Figure 5.

To assess the accuracy of our *a priori* calculation of attenuation due to orientation, we compared the value of η to 1, with 1 being a perfect *a priori* correction factor. We found η to be 0.89, and thus, we believe our *a priori* calculation to remove attenuation effects due to relative orientation was a reasonable estimate.

Random effects

Tag reception and transmission were significant factors in our MCMCglmm, accounting for *ca*. 3 decibels, which should be regarded as the best resolution we can expect in our model. Furthermore, to determine whether the tag's receptive abilities are also reflective of their transmission abilities, we calculated an autocorrelation of 0.97. This finding suggested that the tags' signal reception and transmission are linked.

Predict distance from RSSI using simulations

To classify distances between tags, we developed a simulation that allowed us to separate received powers by distance thresholds. The simulation development contained four steps: 1) creating hypothetical distances between tags; 2) simulating RSSI values for each potential distance; 3) calculating the expected distances to generate error rates in assignment; and 4) assigning error rates at specific distance thresholds.

i) Creating hypothetical distances between tags

To develop a hypothetical distribution of distances between tags (and thus between wild free-ranging NC crows), we considered technological limitations and the behavior of wild NC crows; thus, we modeled a 'realistic' distribution of distances, as this underlying distribution will influence the error rate of our calculations. First, we assumed that close encounters would be more rare than encounters at larger distances, and that the technology would eventually not be able to detect tags after a certain distance. Therefore, we simulated uniform deviates in a two dimensional space,

creating x- and y-axis values through a uniform distribution between 0 and 50 units; we defined our units as 'meters' to match our experimental data and the possible known distances over which tags can transmit. Furthermore, we assumed all tag-to-tag interaction occurred in a planar way (at the same height above ground), but did not specify a height above ground in our simulations. Exact distances were calculated using the Pythagorean theorem, and we simulated one million points. We selected a larger arena than used in data collection because 25 meters is not the range of tag detection; instead we chose 50 meters, a more realistic detection range. Simulating a larger arena is more conservative, as more points at larger distances (between 12.5 meters and 25 meters) will be simulated, giving more power to higher RSSI values at these distances. In addition, the larger arena size has a higher probability of agreeing with our assumption that at large distances, the frequency of received points would be reduced due to a lack of signal detection.

ii) Simulating RSSI values for each potential distance

A RSSI value was simulated for each possible distance according to the following equation:

$$RSSI = N(\kappa - 20\log(d) + \beta * d, \sigma^2). \qquad \textbf{Equation 5}$$

We defined d to be distance, κ as the intercept, β as the slope, and σ^2 as the estimated variance for a given habitat and height through summing all variance components as defined in Table 1. The flexibility to define the number of simulated points for each height and habitat combination allowed us to run multiple scenarios, including a single height and habitat (Figure 4a), multiple habitats at a single height (Figure 4b),

and weighted the proportion of data simulated by the height and habitat by the use of our crows (Figure 4c). Videos were scored to determine the proportion of time that crows spent in each of the habitats, and in the canopy or on the ground; Thus, we demonstrated the changes to our prediction due to habitat and height usage from the animal through data collected from miniature video cameras previously deployed on wild NC crows in the location of our deployment (See Table 2; for reference, see Rutz *et al.* 2007; Bluff & Rutz 2008; Troscianko 2012; Rutz & Troscianko 2012). Two of five habitats could not be explicitly scored, and were placed into the same category; sensitivity analyses were conducted on the simulations to ensure removing either habitat did not substantially alter the distance predictions from RSSI values (data not shown).

iii) Calculating the expected distances to generate error rates in assignment

To predict the distance for all generated RSSI values (and for each of our three scenarios described above), we solved for distance in our equation by setting our equation equal to zero:

$0 = \kappa - 20\log(d) + \beta * d - \text{RSSI}.$ **Equation 6**

iv) Assigning error rates at specific distance thresholds

Two types of error were quantified in our simulations: 1) the number of points that reached our power threshold, but did not reach our distance threshold; and 2) the number of points that did not reach our power threshold, but reached our distance threshold. First, to determine the percent of simulated points that should have occurred within our distance threshold after having met the power threshold, we

divided the number of values incorrectly assigned to the specified distance by the total number of points that were simulated above a distance at which we have arbitrarily assigned a biological meaning. Second, to determine the percent of simulated points that should have occurred within our power threshold after having met the distance threshold, we divided the number of values incorrectly assigned to the specified power by the total number of points that were simulated above the power threshold. In addition, we conducted uncertainty analyses by moving the threshold to include 95% of points within the threshold, revealing the confidence interval of our predictions.

Results from simulations

Using the weighted values from crow cameras, we calculated the probability that a given RSSI value would be assigned to a specific distance (see Figure 5). Specifically, we calculated the probability distributions for three RSSI values, 15, 0 and -20, revealing with 95% of points reliably estimated that the distance is within *ca.* 9, 18, and greater than 25 meters, respectively. Sensitivity analyses conducted for habitat assignment demonstrated a half-meter discrepancy. The probability of a RSSI value representing a certain distance was required to interpret data collected from a deployment of proximity devices on wild animals. After matching a biologically meaningful distance with a distance derived from calibration, a RSSI value can be selected to filter data, and filtering data by RSSI values can be performed to undergo sensitivity analyses.

Discussion

Proximity loggers are being deployed on more taxa to quantify previously immeasurable associations (*c.f.* Krause *et al*. 2013). While the data collected from

these devices address important biological questions, no formal procedure to quantify distance between two deployed tags has been established. In this study, we developed a step-by-step process that can be followed to ensure biological conclusions are limited by the technology's resolution. In doing so, we formalized the conversion of received power to distance, and addressed the variation induced by the behavior of the animal within the environment. While certain limitations remain in our process, such as not explicitly measuring differences in tag power, we recommend that future deployments of proximity tags follow our guide and refine this process.

To capture variation induced by the mobile nature of birds associating at different heights, in various habitats, and regularly changing the orientation of their bodies, we optimized our data collection within methodological limitations (*e.g.*, only being able to sample up to 4 m). We discovered that height is the principal factor contributing to variation (see Figure 4); thus, measured variation of RSSI values will be significantly decreased, and predictive power is increased in future studies that deploy proximity devices on animals maintaining a constant height above ground. Habitat composition explained minimal variation, *c.a.* 3 decibels; but habitats at other study sites containing denser objects (*e.g.*, buildings) may substantially increase signal attenuation. Our model corrected for attenuation due to the relative orientation of antennae, and we discovered that the difference between parallel and perpendicular antennae orientations is *c.a.* 6 decibels. Moreover, deployments not utilizing whip antennae will need to re-calculate this effect and adjust their analysis accordingly.

Within tag variation was statistically significant, implying that tags send radio waves at different power levels; this finding agrees with a previous study using similar tags (Mennill *et al.* 2012), and other studies using comparable proximity devices (Drewe *et al.* 2012; Boyland *et al.* 2013). Thus, the maximum resolution of

distance derived from received power, regardless of signal attenuation due to the environment or the behavior of the animal, is determined by intra-tag variation in power. We recommend that future studies explicitly measure intra-tag variation prior to deployment; this will allow for a *post hoc* correction to remove variation caused by power differences (as performed in Boyland *et al.* 2013).

During our *in situ* data collection, we placed tags at known distances, and measured the received power at each location. A real-world deployment of proximity devices yields RSSI values from which we would need to predict distance. Therefore, we simulated data based upon the fit and error measured from our calibration to develop a predictive framework to understand the range of distances, alongside their probabilities, for each received power. During this process, we assumed that received powers occurred less frequently at high and low RSSI values. Our assumption suggested that at high RSSI values, the probability of being at the correct distance, height, habitat and relative antenna orientation is rare, and at low RSSI values, the technology does not have a constant signal (*i.e.* at far distances, or low RSSI values, a proximity tag is not always in range to receive the pulse from another tag). Future work is necessary to evaluate whether this assumption holds true in all situations.

Calibrating animal-borne proximity devices is necessary for each deployment. While calibrating devices is time-consuming, technological limitations must limit biological conclusions. Proximity devices are not error-proof, rather they exhibit significant variation due to both intrinsic and extrinsic factors; the more factors that must be included due to the environment and/or behavior of the animal, the more variation induced, and the less predictable the actual distance between two tags. While we provide a checklist to aid future calibration exercises for proximity devices, we

recognize that each deployment of proximity devices is unique, and this checklist should be used as a helpful guide to design a proper calibration experimental set-up.

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Table 1: Generalized Linear Mixed Model (MCMCglmm) outputs of projected slope (β), other model parameters, and credible intervals. A MCMCglmm model was fit to data collected at each unique habitat-height combination. The MCMCglmm revealed that attenuation is greater at 0.1 m (approximating the ground) than at 4 m (approximating the canopy). A smaller attenuation effect of habitat was also observed, with more attenuation occurring in denser habitats (*e.g.*, comparing Casuarina and Shrubby at 0.1 m). Since we derived a physical model *a priori* to describe attenuation in a 'perfect' world (*i.e.*, a world with attenuation only due to distance, rather than heights and habitats), we potentially over-estimated the rate of attenuation; this is exhibited in positive values for slope (β).

Parameter	Height (m)	Habitat	Value	95% credible interval	Residuals	95% credible interval (residuals)
β (slope)	0.1	Casuarina	-0.50	(22.35, 25.33)	40.67	(39.67, 41.40)
β (slope)	0.1	Ficus	-0.58	(-0.60, -0.57)	35.21	(34.23, 36.09)
β (slope)	0.1	Gallery forest	-0.27	(-0.28, -0.26)	34.45	(33.75, 35.29)
β (slope)	0.1	Melaleuca	-0.43	(-0.44, -0.42)	31.88	(30.95, 32.57)
β (slope)	0.1	Shrubby	-0.41	(-0.43, -0.40)	34.72	(33.77, 35.41)
β (slope)	4	Casuarina	-0.27	(-0.28, -0.26)	32.10	(31.24, 32.76)
β (slope)	4	Ficus	-0.36	(-0.38, -0.35)	43.65	(42.82, 44.67)
β (slope)	4	Gallery forest	0.03	(0.02, 0.04)	28.83	(28.27, 29.48)
β (slope)	4	Melaleuca	-0.20	(-0.21, -0.19)	34.42	(34.54, 35.20)
β (slope)	4	Shrubby	-0.28	(-0.29, -0.27)	30.76	(29.96, 31.37)
Intersect	NA	NA	23.84	(22.35, 25.32)	NA	NA
η (orientation coefficient)	NA	NA	0.89	(0.88, 0.91)	NA	NA
Transmitting Tag	NA	NA	2.45	(1.12, 4.10)	NA	NA
Receiving Tag	NA	NA	3.82	(1.77, 6.97)	NA	NA
Same-pole	NA	NA	5.24	(2.11, 9.56)	NA	NA

Table 2: The percentage of time New Caledonian (NC) crows occupy different heights and habitats, as measured through video footage captured by miniature animal-borne video cameras. Miniature video cameras were deployed on wild NC crows from 2007 to 2010 in the same study location as the planned deployment of proximity devices (Rutz *et al.* 2007; Bluff & Rutz 2008; Troscianko 2012; Rutz & Troscianko 2012). Videos from these miniature cameras were analyzed for habitat and height usage. Two of the five primary habitats (*Gallery* and *Shrubby*) were difficult to score from camera footage. Thus, to apply these weightings to our simulation, we performed a robustness analysis by assigning either *Gallery* or *Shrubby* as non-visited, allowing the other category to be completely visited. This analysis revealed a one-half meter difference in our predictive ability at close-range encounters, and negligible differences for far-range encounters (data not shown). Because assigning *Shrubby* with the greatest percent-use caused a larger decrease in our ability to predict distance from received power, we conservatively attributed any footage, for which *Gallery* could not be confidently scored, to *Shrubby*.

	Category	Percent
Height	Ground (0.1 m)	10.9
	Canopy (4 m)	89.1
Habitat	Casuarina	4.1
	Melaleuca	54.1
	Ficus	14.8
	Gallery	2.0
	Shrubby	25.0

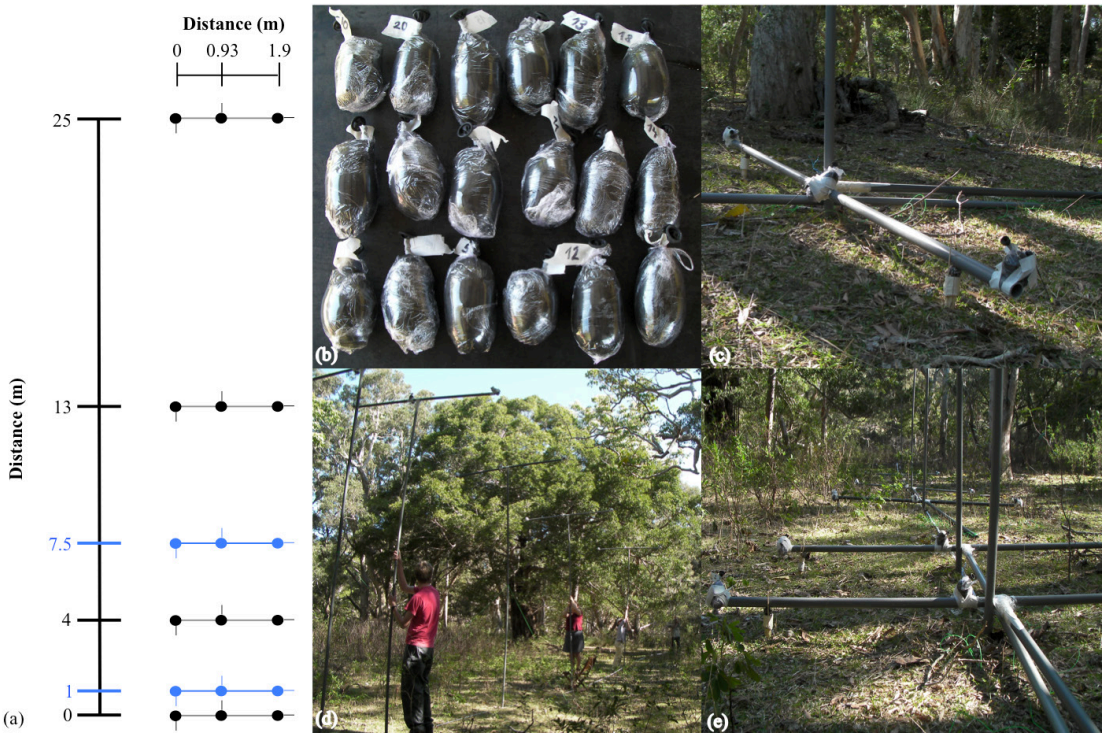


Figure 1. Calibration of animal-borne proximity devices in the natural environment for New Caledonian (NC) crows. We designed a protocol to measure the effect of environmental and behavioral factors on signal attenuation during deployment of proximity devices on wild NC crows. **(a)** A plan view of proximity devices placed on quails (*Coturnix japonica*; solid circles) with different antennae orientations (short lines from solid circles). Quails with attached tags were then mounted on a *c.a.* 2 m PVC pole (long horizontal lines connecting solid circles), and placed at different distances. The relative distance corresponds to the distance between each pair of tags with 0 m acting as an arbitrary starting point to measure distance. **(b)** Tags were mounted on quails, pre-stuffed into balloons to prevent water loss. **(c)** Quails were attached to a PVC pole, with antennae mounted at 45° from the horizontal facing three directions per pole. To quantify variation introduced, two heights, 4 m **(d)** and ground level (*c.a.* 0 m) **(e)**, as well as five habitats, such as a 'gallery forest' consisting of tall 'candle-nut' (*Aleurites moluccana*) trees also

depicted in panel **(e)**, were sampled. Tags pulsed every 20 seconds for 15 minutes at each location.

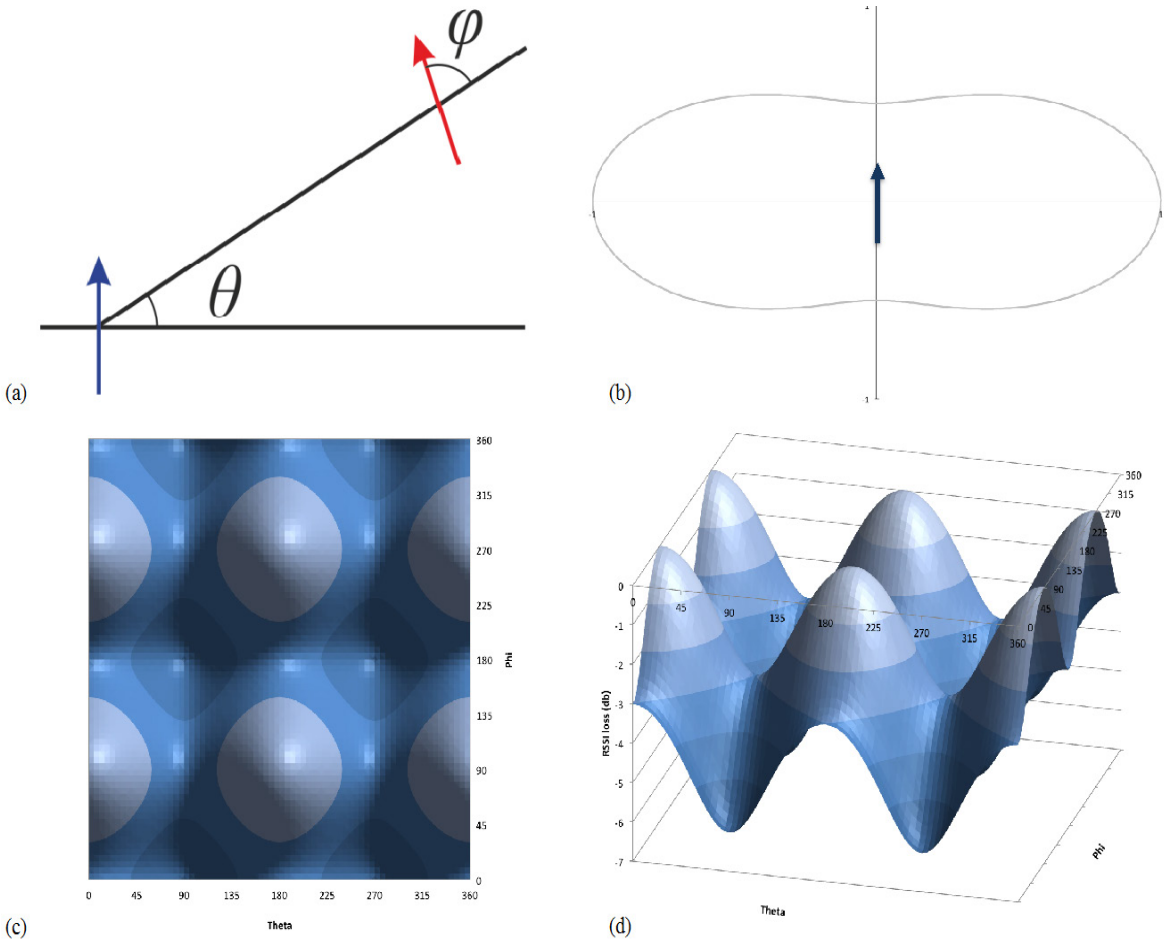


Figure 2. The theoretical attenuation effect of relative tag-to-tag antennae orientation on received power. (a) Arrows depict the facing direction of two NC crows with proximity tags mounted on their backs, with the antennae resting 180° from the front facing direction of the birds. Theta (θ) represents the relative angles in space of the two birds, and phi (ϕ) represents the orientation of the front facing direction of the bird from theta; all angles are calculated with a unit circle surrounding the focal bird, and an angle of zero being to the right of the focal bird. **(b)** The arrow represents the front facing direction of the bird. We assumed that the power radiated to the sides is twice the power radiated in the front and back of the crow. This is represented by the equation $I(\theta) = \frac{1}{2}(1+\cos^2\theta)$. **(c)** Certain angle-combinations of θ and ϕ will cause a decrease in received power of *ca*. 6 db, depicted as the darkest blue, and mathematically represented by $D(\theta,\phi) = \frac{1}{4}(1+\cos^2\theta)(1+\sin^2\phi)$. The darker

the blue, the more signal attenuation is caused due to relative orientation, whereas the lightest blue represents angle-combinations with little to no received power loss. **(d)** The 3-dimensional graph depicts the actual decibel loss for each angle-combination of θ and ϕ, which is mathematically defined as $\delta(\theta,\phi) = 10\log_{10} D(\theta,\phi)$.

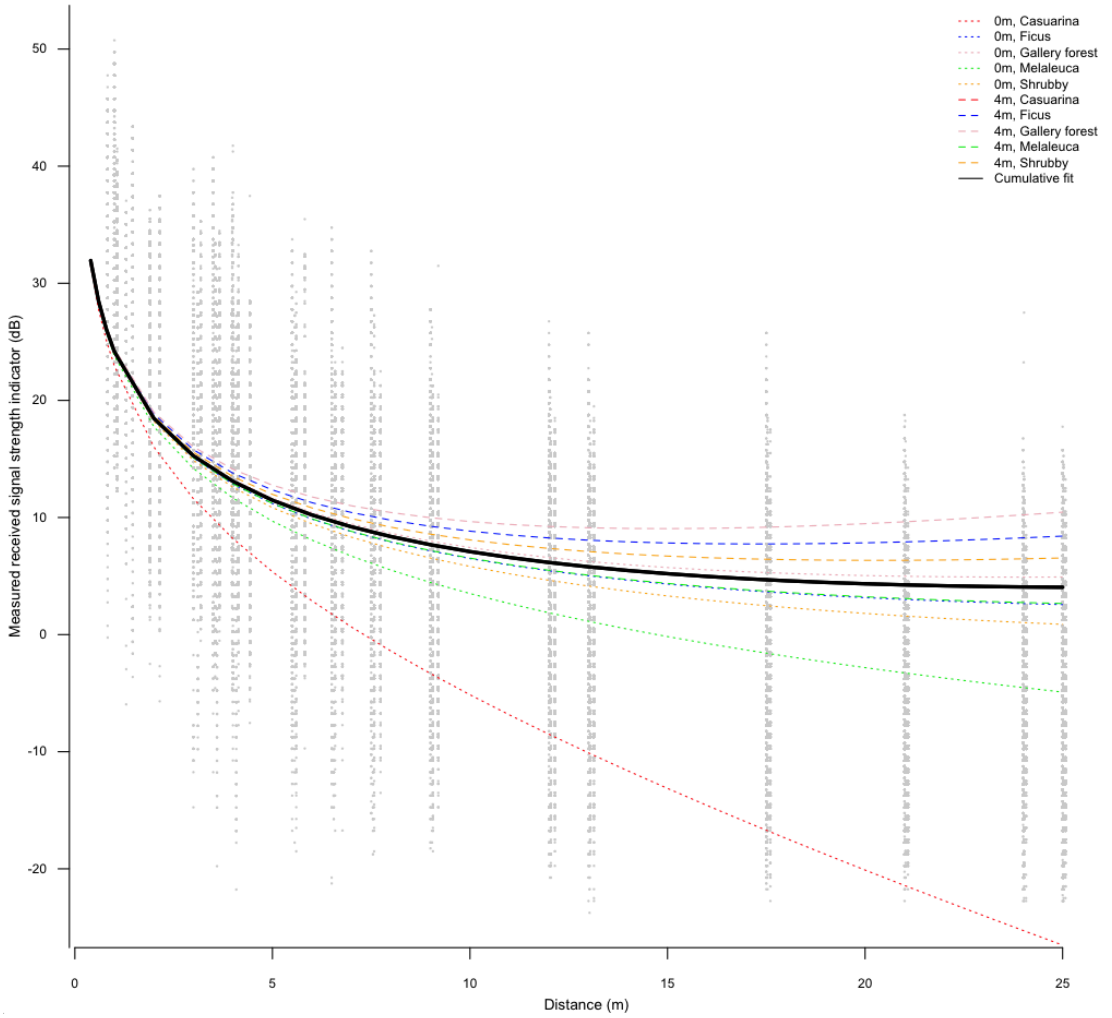
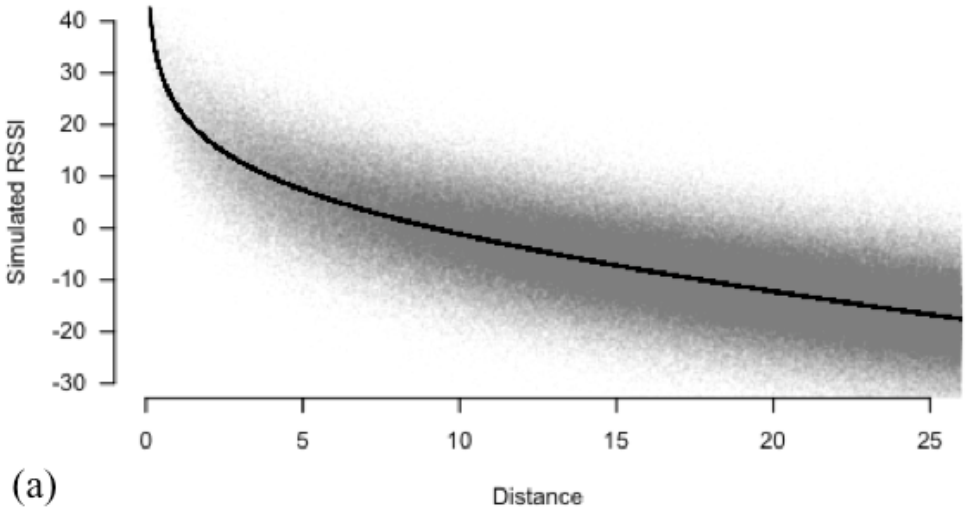


Figure 3. Generalized linear mixed model (MCMCglmm) fits for each height and habitat combination. Data collected from a three-day calibration field experiment (grey dots), and MCMCglmm fits (lines) derived from unique height and habitat combinations, are plotted. Dotted lines depict ground level (0 m), and dashed lines represent the canopy (4 m). The color of the lines denotes different habitats, and is the same for both heights. Only 9 lines are visible because the MCMCglmm fit for 4 m-Casuarina (non-visible) is extremely close to 4 m-Shrubby (visible). 0 m-Casuarina was performed on a slope, therefore, the attenuation on the ground was much higher than other habitats on the ground.


Simulated RSSI
40
30
20
10
0
-10
-20
-30
0
5
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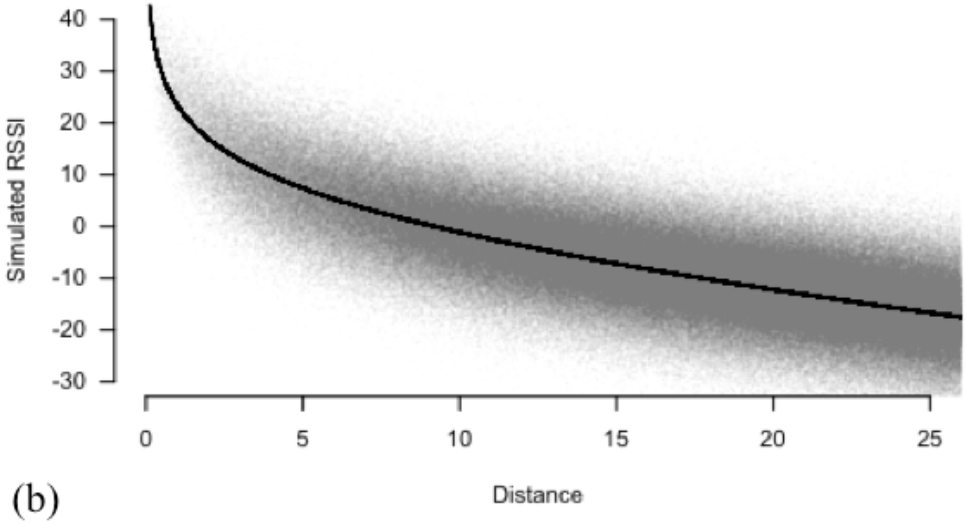
15
20
25
Distance

(a)


Simulated RSSI
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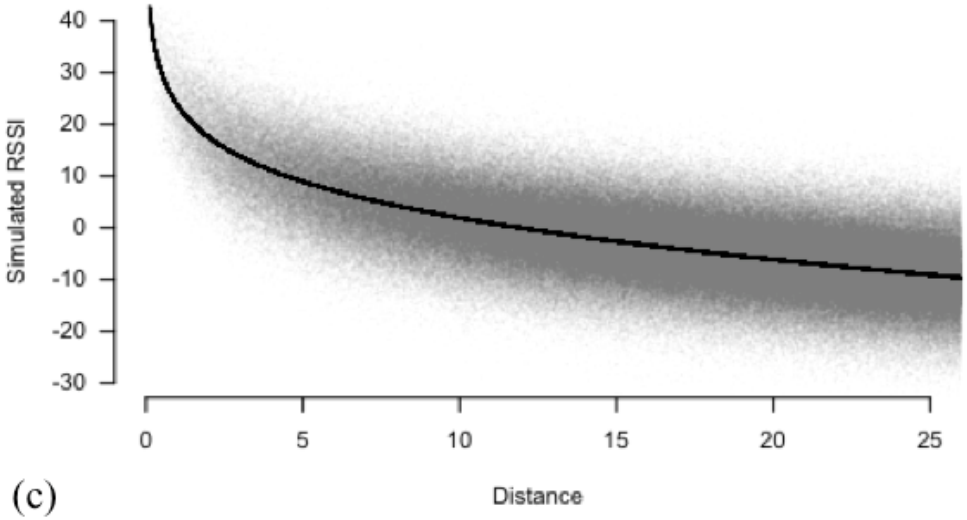
Distance

(b)


Simulated RSSI
40
30
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10
0
-10
-20
-30
0
5
10
15
20
25
Distance

(c)

Figure 4. Three simulations of increasingly complex combinations of height and habitat predict distance from RSSI values. We built three increasingly complex simulations using statistical parameters from data collected *in situ*, with **(a)** a single habitat (Casuarina) at a single height (0 m), **(b)** all sampled habitats at the same height (0 m) with equal probabilities, and **(c)** all sampled habitats at both measured heights (0 m and 4 m) with equal probabilities. Distance is plotted as the dependent variable for ease of comparing these simulations with results from the non-linear mixed effects model of data collected *in situ*. Simulations contained three assumptions: (1) data are homoscedastic; (2) data follow a logarithmic decay; and (3) the probability of a datum appearing is decreased at very close and very far distances, as wild NC crow behavior and technological limitations would reduce the probability of an encounter being recorded at these distances, respectively. The simulated RSSI values were generated by their relative proportion as sampled *in situ*, rather than by probabilistic estimates of NC crow behavior.

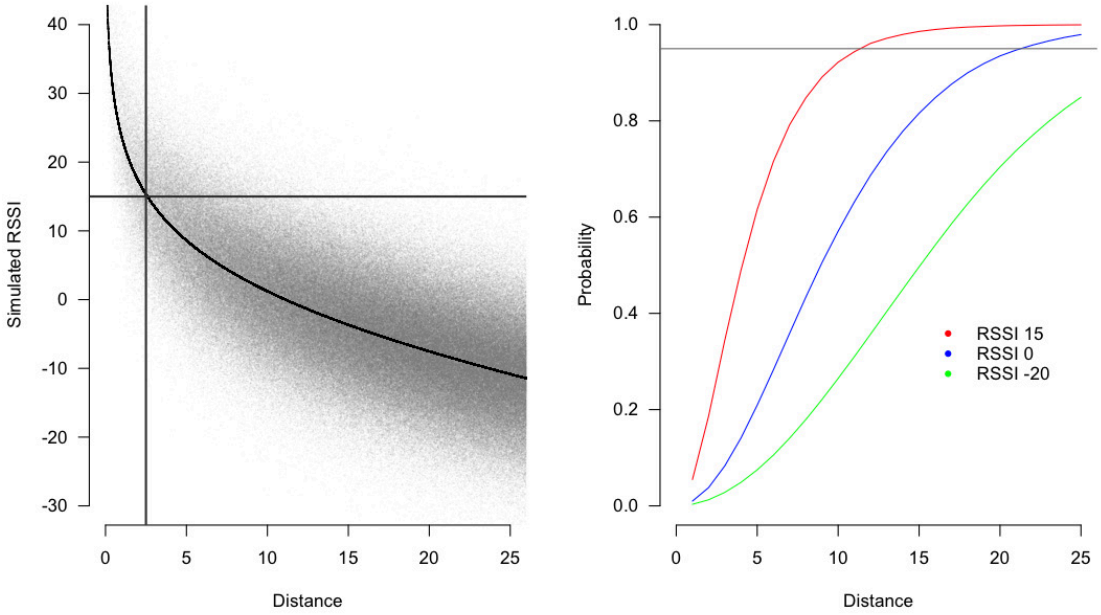

Figure 5. Simulation results weighted by independent observations of NC crow habitat and height use, alongside probability estimates for close-distance (15), far-distance (0), and all recorded encounters (-20). (a) Simulations were generated using the statistical parameters from data collected *in situ* after being weighted by the relative percentages of wild NC crow use of habitat and height. At RSSI 15, 50% of simulated points (or the 'line of best fit') occur at 2.5 meters. **(b)** Depicted is the probability of three chosen RSSI values, 15 (close-range encounters), 0 (far-range encounters), and -20 (all encounters), corresponding to distance; a black line represents 95% probability that the specified RSSI value would be generated within the corresponding distance.

Box 1: Calibration checklist

BEFORE DATA COLLECTION

- ☐ Determine factors that attenuate radio wave signals within the study environment

  e.g., distance, height, habitat, relative orientations of antennae, animal body, etc.

- ☐ Measure the antenna radiation pattern of a tag

DATA COLLECTION

- ☐ Place your tags on objects that closely match the body size of the study species
- ☐ Create a grid of distances and relative orientations for sampling
- ☐ Sample relevant factors from the list created above
- ☐ Measure the received signal strength of each tag under these controlled conditions

ANALYSES

- ☐ Plot your raw data
- ☐ Use a generalized linear mixed model (MCMCglmm) to fit the data, and assess the variation
- ☐ Use the parameters from your MCMCglmm model to predict distance from received power using a simulation
- ☐ If possible, weight your simulation using data about a subject's environmental use
- ☐ Assess the probability of distances generated for each RSSI value, and choose an RSSI value that matches a biologically meaningful distance

CHAPTER 3

A FRAMEWORK TO CLASSIFY ERROR IN ANIMAL-BORNE BIOTECHNOLOGIES (TABLE OF CONTENTS) 67

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A framework to classify error in animal-borne technologies

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Abstract

The use of technology to collect data has steadily increased, especially through the deployment of novel, innovative, and increasingly miniaturized devices on numerous and otherwise difficult to observe taxa. Regardless of progress, every animal-borne device has its shortcomings, such as limitations in precision or accuracy. These shortcomings, here briefly labeled as 'error', are not yet studied systematically, and a framework to identify and quantify error does not exist. Here, we propose a classification scheme to synthesize error across technologies, discussing basic physical properties used by a technology to collect data, conversion of raw data into useful variables, and subjectivity in the parameters chosen. In addition, we outline a four-step framework to quantify error in animal-borne devices: *know*, *identify*, *evaluate*, and *store*. Since mitigating error is essential to answer many biological questions, we believe this process will facilitate future work to determine and quantify error in animal-borne technologies. Moreover, increasing the transparency of error will ensure the technique used to collect data moderates the biological questions and conclusions.

The necessity of animal-borne technologies

Animal-borne technologies (ABTs) collect high-resolution datasets to investigate a wide-range of functional and mechanistic biological questions. From quantifying energy expenditure in migrating geese (*Branta leucopsis*; Butler *et al*. 1998) to measuring the sociality of wild tool-using crows (Rutz *et al*. 2012), ABTs are resolving questions at a steadily increasing resolution (*c.f.* Shillinger *et al*. 2012). In addition, ABTs allow measurements on difficult to observe fauna, such as examining sea turtle feeding and breathing at sea (Okuyama *et al*. 2009) or

observing the conservation and social dynamics of reintroduced wolves in Yellowstone National Park (*Canis lupis*; Fritts *et al*. 1997). Furthermore, ABTs have mapped the spatial associations and exchange of tuberculosis between cattle (*Bos primigenius*) and badgers (*Meles meles*), demonstrating the importance of animal-borne technologies in informing policy (Böhm *et al*. 2009).

As quantification progresses in an increasing number of species, and as we collect more complete and robust data, the cycle of ABTs stimulating new biological questions alongside existing biological questions driving innovative ABTs will increase. Since the mid-twentieth century, ABTs have become integrated into the core of animal-focused research, such as animal behavior, ecology, and conservation (Brown *et al*. 2013). We believe this broadening will continue to expand the use of ABTs in biological research, leading to a strong reliance on ABTs to resolve prevalent questions. As more studies utilize ABTs, and a considerable amount of effort is invested in storing and combining various kinds of data, ensuring data collection protocols consider limitations and measurement errors become imperative (*c.f.* Krause *et al*. 2013).

Error in animal-borne technologies

Understanding and quantifying error is essential for discovery. Random and systematic error obscures the relationship between two variables, making it difficult, or even impossible, to collect sufficient evidence to reject a null hypothesis. Biases can, when unrecognized, lead to the acceptance of incorrect hypotheses and/or the identification of erroneous models. And even when error is recognized and properly modeled, lack of precision decreases the statistical power of a study and increases the likelihood of missing a significant biological outcome.

Thus, identifying sources of error *a priori* is essential to maximize the outcome of a study. While some sources of error have been investigated, such as the environmental effects on Argos (a type of satellite transmitter; Patterson *et al*. 2010), the impact of the physical size of devices on Penguins' swimming performance (*e.g.*, speed recorders on *Spheniscus demersuse* by Wilson *et al*. 1986; time-depth recorders on *Eudyptes schlegeli* by Hull 1997), or the variation of GPS location accuracy and fix rate with vegetation and antenna position (Jiang *et al*. 2008), we believe and concur with other studies (see Friar *et al*. 2010) that most sources of possible error have neither been identified nor quantified.

We believe that the lack of error quantification in ABT studies is due to three factors. First, the study of device error will not directly lead to finding exciting biological phenomena: in fact, researching error comes at the cost of 'real' discoveries in terms of time and resources. Moreover, studies at the interface of technology and biology could not be easily published due to the dearth of methodological journals. Second, progress in observation frequency and accuracy of ABTs are so big relative to conventional methodologies (*e.g.,* observations with binoculars) that device error is not the primary concern. Rather, sample size, automated processing, and correct analytical techniques for ecological interpretation were given a higher priority. Finally, a framework to explore and quantify possible errors in ABTs has been lacking.

While we believe that the first two causes for the limited attention are disappearing as new interdisciplinary and methodological journals have been founded (*e.g., Journal of the Royal Society Interface* or *Methods in Ecology and Evolution*), a general framework to discuss and analyze error has not yet been established, though some previous studies focus specifically on error within a single

device, such as GPS (Friar *et al*. 2010) or accelerometers (Shamoun-Baranes *et al*. 2012).

A new framework for error

Prima facie, each technology has a unique set of pathways by which error is introduced; thus, we believe that these errors can be categorized by the processes that introduce the variation. We propose that there are three fundamental concepts that, when used to classify error, enable a comprehensive evaluation of error, regardless of technology: 1) the basic physical properties underlying data collection; 2) the conversion of raw data into useful variables; and 3) the subjectivity in the selected settings. We believe the use of this classification system will facilitate future work to recognize additional sources of error and, subsequently, to propose practical ways to mitigate and/or statistical methods to quantify error. Here, we outline and discuss this classification scheme (see Box 1). We do not attempt to review the literature exhaustively; rather, we discuss numerous technologies to demonstrate the breadth of technologies that will benefit from this categorization.

Basic physical properties underlying data collection

All ABTs utilize physical properties to function: encounter mapping devices, RFID tags, and GPS devices all transmit and/or receive data through radio waves (varying from low to ultra-high frequencies), geo-locators detect fluctuations in light intensity (see Box 2), and accelerometers record changes in capacitance. While each technology measures a unique property or transmits data through a unique method, each physical property has generalizable characteristics, uncertainty in their measurement, and identifiable limitations.

For example, encounter mapping devices use radio waves to transmit unique animal IDs between tags. As radio waves spread in an environment, the energy contained within the radio wave decreases at a certain rate, and extrinsic factors, such as height above ground or the composition of the habitat, can alter this rate. Thus, as performed in Chapter 2, a calibration to determine the rate at which radio waves degrade due to the behavior of the animal is essential.

Similarly, GPS devices transmit and receive ultra-high frequency radio wave signals from satellites. If any medium, like a vegetation canopy, is obstructing the travel path of the radio wave towards the sensor, resulting in a lower fix rate and lower number of satellites that can be detected – hence a lower location accuracy. Therefore, GPS devices require a calibration (as done in Jiang *et al*. 2008, see Friar *et al*. 2010 for a more complete overview) to distinguish differences in performance under different types of vegetation so that seemingly different intensities in habitat utilization by an organism can be interpreted accurately.

Radio waves degrade at a specified rate (different rates for different frequency of radio waves), and certain extrinsic factors, such as height above the ground, can distort the signal (Chapter 2). Studies have quantified the degradation and variation of the signal due to external factors of signal strength and/or reliability. Devices utilizing radio waves have significant variation in signal strength, suggesting that using these devices to differentiate distances may be problematic.

Conversion of raw data into useful variables

When using ABTs, the biological outcome is only as good as the conversion of raw data into useful variables. Three steps are generally taken during this conversion:

(1) understanding the structure of the collected data, (2) determining the relationship between the raw data and the variable of interest, and (3) quantifying the error associated with the conversion. While many studies undertake steps 1 and 2, few studies have concentrated on quantifying error from the conversion of raw data into useful variables.

Light based geo-location sensors, 'geolocators', convert incoming light levels into electrical energy to match to an internal clock to determine location. To convert the light level to the date-time information, a deterministic model (relating the time of local noon and midnight to the latitude, and day length to longitude) is used. Usually the incoming light is limited to the 450 ± 50 nm wavelength (a light-blue filter), because blue light predominates at the sun angles most appropriate for geo-location, just before sunrise and just after sunset (*e.g.,* Lisovski *et al*. 2012). In addition to this well understood deterministic part of light based geo-location, there are large uncertainties involved due to factors such as clouds, atmospheric refraction, atmospheric dust loading, foliage, feathers, depth, or temperature effects (Eckstrom 2004, Fudickar 2011, Lisovski *et al*. 2012). Some of these factors can be corrected by measuring additional variables (such as pressure and temperature for aquatic animals or cloud coverage at weather stations), whereas others have to be factored in as sources of error. Several studies have been conducted to establish the uncertainty introduced by these factors, and provided a protocol to calibrate sensors prior to deployment (Eckstrom 2004 and Fudickar 2011).

A recent methodological analysis highlighted the error associated with converting the received power from an incoming radio wave signal into a measurable distance between two individuals (Chapter 2). While this study revealed that extremely close distances, within approximately a few meters, were

differentiable from tens of meters, the study highlighted the limits of differentiating distances greater than *c.a.* 10 meters. Moreover, this study demonstrates the necessity to understand the conversion of raw data into useful variables, highlighting the large error associated in this conversion; and demonstrates that only a few extrinsic factors must be considered to decrease the variation associated in the conversion of received power to distance.

Subjectivity in the settings chosen

Nearly all animal-borne technologies necessitate *a priori* selection of certain parameters. Generally, selecting parameters involves balancing the trade-offs between the highest resolution possible and the technological limits of the ABTs, such as in the accessible memory and/or the capacity of the battery. Throughout the last decade, we have seen steady improvements in on-board memory and battery lifespans (Rutz and Hays 2009), and may eventually see these limitations become nonexistent.

One key parameter chosen is the frequency at which data is recorded. The rate of data collection determines the level of analysis that data can be quantified, with higher rates of data collection allowing more *a posteriori* grouping of data for analysis, an indispensable step (at least for now) to analyze the data. For example, if we collect data every second, we may be able to group data every ten seconds, and test hypotheses that require changes in the tens of seconds. It is important to note that we should maximize the rate at which we collect data, as analytical methods allow for the comparison of higher-resolution data with older, less resolved data.

Another parameter commonly chosen is the power at which devices operate. In systems with passive RFID tags, for instance, the power of the receiver

determines the distance (and rate) at which tags are being recognized. Since the detection range can, as a function of power, vary over an order of magnitude, knowing the exact power setting is crucial to understand the impact of this variability in measuring the detection range (Finkenzeller 2010). Hence, the standardization of procedures in this context, or the availability of general calibration curves, are required to compare results from different studies or interpret the results from a focal study (*e.g.,* Pinter-Wollman *et al*. 2014).

Towards a universal method

Each technology has its own unique limitations, necessitating different analytical or methodological approaches to mitigate error due to technological constraints. Even though limitations exist in numerous technologies, increasing the transparency through a common scheme will facilitate more rigorous studies and ensure the technological limitations refine and restrict the biological outcomes. Therefore, we outlined a process to facilitate a common method to think about error systematically, which we hope will facilitate more quantification of error.

Our process (*i.e.* to know, identify, evaluate, and store) alongside the three processes introducing error into our data collections (*i.e.* physical properties, conversion from raw data into useful variables, and subjectivity in the settings) will increase the transparency of future work deploying animal-borne devices. Our design ensures the investment of time and energy elucidating methodological concerns benefits all future studies deploying animal-borne devices. Altogether, the adoption of this scheme will ensure our biological conclusions are formed in light of rather than as a consequence of the methods used to collect the data.

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Glossary:

Accelerometer: a device that measures the acceleration experienced by a test mass at rest in a reference frame in a single or multiple dimension(s). Multi-axis acceleration detects magnitude and direction of the acceleration as a vector quantity, and can be used to sense orientation. An accelerometer measures change in its own motion (locomotion) instead of the location within the environment (devices based on remote sensing).

Acoustic device: a device commonly used in aquatic environments, working through the transmission of a sound signal that is received subsequently by an array of hydrophone receivers. The location of the device can be estimated from the relative arrival times to the receivers. The sound signal is unique for each device so that each device can be identified.

Encounter mapping devices (EMD): a range of devices, such as GPS, proximity, or acoustic, used to map associations either directly or indirectly between objects.

Global positioning system (GPS): a satellite navigation system developed and managed by the United States military, consisting of 24 satellites above the earth and transmitting ultra/very high frequency (UHF or VHF) radio signals to receivers. The receivers compute longitude, latitude, and velocity by calculating the difference in the time signals are received from at least four different satellites.

Proximity sensor: an animal-borne device that detects the signals of other devices, including mobile tags, static transmitters/receivers, or human-operated elements

(*e.g.*, yaggi antenna). To transmit the device identity, these devices currently use radio waves, and the receiving tag detects the power of the received pulse to record the encounter, alongside the time of the association. Future devices may use other forms of transmission.

Radio frequency identification (RFID) system: an automatic identification and data capture system comprised of one or more readers, and one or more transponders (tags) through which data transfer is achieved by means of suitably modulating inductive or radiating electromagnetic carriers. An RFID reader transmits an encoded radio signal to interrogate the tag. The RFID tag receives the message, and then responds with its identification and other study related data.

Random error: unpredictable fluctuations in observations due to the precision limitations of the measurement device, variations in the measurement procedure that is applied, and/or heterogeneous environmental conditions. Random errors are on average zero. The variance of the fluctuations can be estimated, but it cannot be corrected.

Systematic error: systematic deviations of measurements from the quantity meant to be observed due to the functioning of the measurement device, the measurement procedure that is applied, and/or the environmental conditions. Systematic error can, when understood, be corrected by, for example, a calibration equation.

Box 1. The four steps: Know, Identify, Evaluate, and Store

Our procedure is based on 4 steps, which we labeled 'Know', 'Identify', 'Evaluate', and 'Store'. Knowing consists of: 1) the physical principles of the technology, 2) the limitations of the technology, 3) the specific device and the context (*i.e.* the environment in which the device will be applied), and 4) experiences from others using the same device under comparable conditions. Knowing about the physics, sensor specification and context will enable a researcher to assess the likely sources of error in the specific location(s) the technology will be used. Knowing these sources of error is a required input to the next step: identify.

After knowing the sources of error, a two-step process to 'identify' the proper model is necessary: 1) building a model from first principles, and 2) parameterizing this model with collected data. First, if possible, the physical model should be defined on the basis of first principles (*e.g.,* the effect temperature has on the functioning of a certain circuit, or the attenuation of a wave through a homogeneous medium at a given temperature). The physical model is constructed to describe the relationship between the variable of interest, the relevant environmental factor(s), and the variable that is actually recorded by the device. In some cases, the physical model is sufficient to move on to step three, however, in many cases, further parameterization with empirical data may be required, as shown in Chapter 2. For those cases in which the physical model is already derived, collecting data *in situ* and parameterizing the model are the only steps required. In both cases, either the physical model or the model parameterized with collected data is ready for step 3 of the process.

To establish the robustness of the model in heterogeneous conditions, step 3, 'Evaluate', is completed through a sensitivity and uncertainty analysis. For a

sensitivity analysis, no real observations are required. Parameters or inputs are varied to evaluate the model's robustness to perturbations. A sensitivity analysis is useful to find the parameters or inputs for which the observation model is particularly sensitive; these may subsequently be investigated in an uncertainty analysis. An uncertainty analysis applies variability to a model to investigate the propagation of uncertainty with the potential to modify the outcome. If the resulting uncertainty is acceptable, the model is ready for use. In many situations, the model will work only within certain boundaries of input parameters. To ensure proper re-use of the model, specifying the conditions in which the observation model performs or does not perform well is essential.

Finally, we must properly store the model, and we must make publicly available the code used to generate the model. With a simple parametric model one can store parameters alongside their uncertainty. But with non-parametric models, we should store the complete calibration dataset and algorithm; in that case, model uncertainty needs to be expressed in terms of predictive uncertainty. Importantly, the assumptions underlying the model and limits of the models application must be stated. We strongly believe storing the model with uncertainty is essential to facilitate its future use.

Box 2. Geo-locators: the epitome of error in animal-borne devices

Geo-locators calculate location using ambient light-levels, solar irradiance, at a given time. Longitude is estimated from the time of the local midday (or midnight) relative to Greenwich Mean Time (GMT), and latitude is determined through the length of the day (or night). Geo-locators have improved our understanding of numerous biological systems, especially at-sea movements of diving birds (*e.g.,* Boost *et al*. 2009). While the miniaturization of geo-locators has enabled long-term deployment, extensive understanding and quantification of error is essential (and in many ways, impossible).

Numerous types of error inhibit our biological interpretation of the raw data collected (Wilson *et al*. 1992, Hill 1994, Teo *et al*. 2004, Ekstrom 2007, Thiebot and Pinaud 2010). A standard method to filter data includes 'rejecting unrealistic estimates, especially during equinox periods' (Thiebot and Pinaud 2010). During the two to three weeks surrounding the equinox, the day length is equal everywhere on earth; thus, determining latitude or longitude has low to no accuracy. In addition, different factors, such as cloud cover, artificial light sources, shade, pollution, latitude, season, adjustment of the device, and behaviors of the studied animal cause light attenuation, limiting our ability to trust the raw recorded data. A recent study investigated the accuracy of geo-locators by ground-truthing the location in a tropical rain forest (McKinnon *et al*. 2013), suggesting that the best latitude estimates in the tropics are from the dry season locations. Altogether, numerous factors have been quantified to reveal sources of measurement error.

Since geo-locators have numerous sources of error, much of the focus of these devices has been to know the sources of error, to identify a quantitative process to understand the role of error, to evaluate whether the error effects the

biological conclusion, and to store algorithms for others to evaluate and understand the contribution of error to their recorded data. For example, a recent study (Thiebot and Pinaud 2010) developed a quantitative method to determine habitat use based on light-based geo-location data. Specifically, this study identified known errors, evaluated the errors, and stored their developed algorithms as functions in a free online platform for statistical computing, 'R' (R Development Core Team). The process utilized by users of this device and presented here in this study ought to be widespread in the evaluation of biological outcomes from animal-borne devices.

Table 1. Methodological characterization of animal-borne technologies.

Technology	**Basic physical properties**	**Raw data to useful variable**	*Influential factor(s)*	**Subjectivity in parameters**	**Example**
Accelerometers	Acceleration	Acceleration to behavior Acceleration to displacement (trajectory shape) Acceleration to energy	*temperature*	Known reference position Log frequency Stability of sensor	Brown *et al*. 2013
Acoustic	Sound waves	Delay in arrival to distance*	*configuration; hydrophone; salinity; temperature*	Pulse length	Ehrenberg and Steig 2002
Geo-location	Light intensity	Timing of sunrise and sunset to position	*shielding of antenna; vegetation; weather*	Light threshold or parameters in light-interpolation models	Fudickar *et al*. 2012 Bridge *et al*. 2013
GPS	Radio waves (L1:1575.42 MHz; and L2: 1227.6 MHz)	Delay in arrival to distance*	*atmosphere; configuration; reflections; satellite; shielding of antenna*	Atmospheric properties Reflectance	Williams *et al*. 2012
Proximity	Radio waves	Received power to distance*	*antenna; directionality operating power; vegetation*	Threshold of received power	Rutz *et al*. 2012
RFID	Radio waves	Tag identification	*Antenna; directionality; vegetation*	Power setting of recording station	Nikitin and Rao (2006)
Time depth recorder	Pressure	Pressure to depth	*temperature*	Log frequency Threshold depth	Hays *et al*. 2007

* And subsequently a translation of various distances (to receivers at known location) to location via triangulation

Discussion of Section 1

Overall, I have quantified error in an animal-borne device, *Encounternet*, and outlined a framework to facilitate other studies to explore error systematically regardless of device. The last two chapters demonstrated that quantitatively exploring the error in animal-borne devices is an extensive process that requires collaboration between biologists, statisticians, and physicists to develop a comprehensive pathway for studies to ensure the error in their devices is considered and limits their biological conclusions. Importantly, all future deployments of animal-borne devices must incorporate a proper error assessment into their work.

Throughout the next section, I utilize the distance-to-RSSI conversion quantified in Chapter 2, to define distance. However, I use the RSSI value, rather than distance, to more clearly resemble the data collected. This is important because the process shown in Chapter 2 produced a range of distances at which a certain probability of the received power being that distance or closer was prescribed. Therefore, in the following section, the distance for each RSSI value can be found in Chapter 2.

Section 2: Empirical Experiments

Introduction to Section 2

Built upon the analyses, limitations, and outputs of Section 1, this section explores the social network and information exchange potential of wild NC crows. Since wild NC crows are well known to be difficult to observe directly, we deployed the *Encounternet* technology as described above to measure who associates with whom.

This section has two major themes: direct and indirect potential for information exchange. In Chapter 4 and Chapter 5, I explore the social networks of wild NC crows through four experimental time periods to reveal dynamic changes due to experimentally placed food gluts. In Chapter 6, I explore a caveat of using RSSI to measure an experimental protocol, and discuss the technological limitations due to environmental-based signal attenuation. In Chapter 7, I explore whether NC crows prefer inserted tools over 'sticks' resting on the foraging apparatus, test whether the tool's insertion drives the preference, and determine whether the inserted tool is preferred when compared to an environmental cue. In Chapter 8, I combine the social network analyses presented in Chapter 4 and Chapter 5 with the use of abandoned tools (Chapter 7) to quantify the number of social partners that correspond to shared space: I calculate the number of individuals that could have exchanged tools indirectly.

Altogether, I aim to quantify for the first time the social network of wild NC crows using an animal-borne device. Furthermore, I seek to correlate different factors that could drive NC crow sociality: genetics, environmental perturbations, and the use of the environment.

CHAPTER 4

MAPPING SOCIAL NETWORKS IN WILD NEW CALEDONIAN CROWS

This is a narrative chapter with a majority of data derived from a published paper (Rutz *et al*. 2012- See Appendix 1) with additional analyses.

Abstract

Quantifying the structure of animal social networks has uncovered numerous biological outcomes, such as revealing the genetic or spatial structure underlying who associates with whom. Yet, recording high-resolution association data, especially for small animals, has proven to be a limiting step towards advancing our understanding of the drivers of association patterns in wild populations. Here, we successfully deployed a novel transceiver and data logger to map associations of wild New Caledonian (NC) crows, *Corvus moneduloides*. NC crows are suspected to transmit tool-related information, thus investigating with whom each individual associates will advance our understanding of direct associations on cultural transmission. We analyzed over 28,000 association logs, revealing more social partners than their immediate family, contradicting the predictions from a previous study. Altogether, these data suggest that the potential for wild NC crows to use social information from non-related peers and other adults may be greater than originally suspected.

Introduction

Animal-borne technologies increase our understanding of animal populations by measuring their behavior, associations, or space use *in situ* (Krause *et al*. 2013). Since the advent of radio-telemetry in the late 1950s (*c.f.* Kenward *et al*. 2001), technologies have steadily improved (Rutz and Hays 2009), and are becoming increasingly autonomous with data being either stored onboard or transmitted autonomously to a receiver. Moreover, animal-borne devices are highly dependent on better batteries, since an increase in battery life allows for higher resolution data capture and longer deployments. Over the last decade, we have witnessed numerous

technologies become miniaturized, such as video cameras being deployed on wild New Caledonian crows (*Corvus moneduloides*; hereafter, NC crows; Rutz *et al*. 2007).

Yet, through these advancements, most animal-borne devices that measure association patterns have remained too heavy for deployment on small animals, have limited detection ranges, and/or require the device to be retrieved to download data (Rutz *et al*. 2012a, Rutz and Hays 2009, however, see for reference Aplin *et al*. 2012). One device capable of being deployed on small animals, RFID/PIT devices (passive tags that are registered by receiver stations when the animal comes within a certain distance), overcome the weight limitation, but are limited to species that reliably go to certain locations for specific tasks, such as foraging or mating. For example, RFID/PIT tags have been deployed on three species of tits (family Paridae) to investigate their habitat usage and habitat quality (Wilkin *et al*. 2009), and their social networks (Farine *et al*. 2012). Altogether, the limitations of animal-borne devices, except RFID/PIT tags, have restricted our ability to study small wild animals, such as passerine birds.

Understanding the decisions of wild animals are essential to chart their social structure, or the organization of individuals within a population (Hinde 1976). One increasingly common method to quantify the social organization of animals is social network analysis (*c.f.* Croft *et al*. 2008). While standard field methods, such as direct observation using binoculars, can quantify population dynamics using network analysis, data from animal-borne devices allow for undisturbed measurement of behavior and higher resolution data collection (Krause *et al*. 2013). Moreover, rather than using the 'gambit of the group', or having statistically dependent data due to collecting data on associations only in groups, to measure

associations, animal-borne devices facilitate the recording of fission-fusion events in real-time, such as capturing decision making processes that can be traced to specific environments and social activity (James *et al*. 2009). Thus, analyzing data from animal-borne devices through social network analysis can prove extremely powerful in advancing our understanding of wild animals (Krause *et al*. 2011).

NC crows are prolific tool-users and manufacturers suspected of acquiring tool-oriented information from conspecifics (Hunt and Gray 2003). NC crows have been shown to use tools in logical sequence (Wimpenny *et al*. 2009) and in context dependent situations (Taylor *et al*. 2012), and even attend to the functional properties of their tools (St. Clair & Rutz 2013; however see Holzhaider *et al*. 2008). Altogether, these observations have led multiple studies to state that NC crows demonstrate the most sophisticated tool-oriented behavior amongst birds, and that their tool-use and manufacture rivals that of Chimpanzees (*Pan troglodytes*; Hunt 1996; Hunt & Gray 2003; for a review, see Rutz & St. Clair 2012, however see McGrew 2013). Yet, little is known about the social lives of wild NC crows, a necessary step towards quantifying from whom tool-related information could be acquired.

Much of the information gathered about the sociality of wild NC crows stems from observations at feeding tables (Holzhaider *et al*. 2010, 2011, Hunt *et al*. 2012). From these observations, a social family emerged as the core unit of social organization, with a pair-bonded adult pair, a juvenile crow, and sometimes the juvenile from the previous year (Holzhaider *et al*. 2011). Moreover, the pair-bonded adult crows pair for multiple years; in one case, upon the death of the female adult's male partner, this female NC crow re-bonded with another adult male (Holzhaider *et al*. 2010, 2011). Importantly, the newly pair-bonded unrelated adult male spent

significant time with the adult female's offspring; no observations of provisioning were recorded and agonistic interactions were not frequent (Holzhaider *et al*. 2011). From this work, Holzhaider *et al*. (2011) predicted that the social network of wild NC crows includes very few social partners outside of their social family.

Here, we used a novel animal-borne device, proximity loggers (devices that transmit radio-waves between tags) to quantify the network of wild NC crows. First, to ensure tags were functioning properly, since this was the first deployment of these tags on wild animals, we quality checked tag properties, such as continuity of pulses, tag-resets, and clock drift. Next, to determine whether the population contained sub-units of organization, we applied four community detection algorithms to search for structure. Finally, to measure basic properties of the network, we calculated the number of social partners and the duration of pair-wise encounters. Altogether, we aimed to characterize the social structure and network of a population of wild NC crows.

General Methods

Encounternet

Three components comprise *Encounternet*, the direct proximity logging system, that maps associations: (1) animal-mounted 'tags' capable of transmitting, receiving, and logging data; (2) environment-deployable 'basestations' capable of transmitting, receiving, and logging data; and (3) 3-element Yagi antennae, or 'masternode', capable of transmitting, receiving, and archiving data (See Figure 1). Custom software, alongside a novel hardware design, allow for all components to communicate with one another. Furthermore, deployed tags and basestations can be re-programmed provided that the 'masternode' is within communication range,

which often occurred to check the status of clocks (and thus calibrate or reset the clocks), and the number of logs on each tag (or to download if we wanted to undertake real-time analysis).

Tag settings

Encounternet enables specific components to be programmed to maximize the system's performance, a key limitation of earlier technologies (Rutz and Hays 2009). To balance the resolution for mapping associations over time and battery limitations (the length of deployment), tags were programmed to pulse every 20 seconds at 433 MHz. Furthermore, to save battery, we programmed our tags to turn on each morning at 4:00 (sunrise approximately 5:00), and off each night at 20:00 (sunset approximately 19:00), allowing for all daytime associations, and the beginning and end of roosting to be recorded.

In addition to battery constraints, onboard memory capacity also constrained programmable components through balancing the resolution of potential association dynamics, and ensuring the tag memory was never full. When a tag received a pulse from another tag, the tag created an encounter log, and recorded the date and time of the incoming pulse, as well as the power of the pulse. As more pulses reached the tag from the same individual, the pulses were combined into a single log, for up to 300 seconds, a programmable interval, eventually containing a time of first encounter, the time of the last pulse received, and a minimum, maximum, and mean power received (see chapter 2).

Basestation settings and deployment

Basestations were neither battery nor storage limited, since four D-cell batteries powered the basestations and the SD card could contain over a million encounters. Thus, all basestations recorded every pulse from a tag within range. Moreover, basestations downloaded encounter logs from tags, to ensure free tag memory remained low in case a bird moved away from the basestation grid, and was still producing encounter logs. Basestations were programmed to download data from tags after 60 encounter logs stored in the core or 18 encounter logs were stored in the periphery of our study area. Encounter logs were collected from basestations (and tags, if necessary). Real-time analyses were undertaken to ensure tags were within range of basestations during some part of the day, allowing for close monitoring of data-collection to ensure tags never reached free memory capacity, and that basestations were regulating the collection of data from tags properly. Forty-five basestations were mounted in the tree canopy following the topography of two riverbeds located in each of two-valleys, balancing data collection with the recording of each NC crow's space-use.

NC crow trapping, sexing, relatedness, and tag mounting

Forty-one NC crows were trapped at four locations in our long-term dry forest focal study site on the central west coast of Grande Terre, New Caledonia (See Taro and Tabou valleys in Rutz *et al*. 2007, 2010, Bluff *et al*. 2010). Crows were captured from 2 to 21 October 2011 using whoosh nets baited with meat. Captured NC crows were weighed, measured, and marked with rings and wing-tags. Blood was collected from each bird for sexing, and genetic relatedness, as performed in Kenward *et al*. 2004. The age of each NC crow was determined from the percent of

black that appeared in the gape coloration as it changes from pink to black (see Heinrich and Marzluff 1992).

Afterwards, we mounted *Encounternet* tags using 'one break–all release' designed harnesses (1.5mm braid for large individuals, 1.2mm braid for small individuals; Sirtrack Ltd., NZ). This design was used in a previous VHF radio-tag study on this population (*c.f.* Rutz *et al*. 2012), as well as on another population of NC crows (see Holzhaider *et al*. 2011). To ensure animal welfare, previous studies had successful deployments, no reported incidents of bodily harm for birds, and within our population, tags were known to fall off safely with a high probability after several months (Rutz *et al*. 2012).

Encounternet is lightweight enough to be deployed on wild NC crows, overcoming a key constraint in deploying similar technologies on NC crows. Direct proximity technology developed by Sirtrack (Prange *et al*. 2006) weighs *ca*. 10% of a NC crow's body weight (*ca*. 300 g as per Kenward *et al*. 2004), and when fully packaged for deployment with a collar, weighing between *ca*. 10% and 30% of a NC crow body weight. This far exceeds the recommended 3-5% of body weight for long-term deployments (Rutz *et al*. 2007). Our tags weighed 9.57 g ± 0.050 (mean ± SE), with a range from 8.90 g to 10.21 g, amounting to 3.35% ± 0.062 (mean ± SE) of NC crow body mass, with a range from 2.65% to 4.07%. Harnesses (weighing 1 g for small and 2g for large) were individually fitted to each NC crow with the *Encounternet* tag; the weight of the tag and harness never exceeded the safe limit of 5% of a NC crow's body mass.

Data collection

Tags were programmed to 'sleep' (not pulse) until 27 October 2011 at 4:00am, at which time the tags would begin pulsing every 20-seconds; The sleep mode allowed for a 5-day no-trapping period, during which only basestation deployment occurred, and for the population to return to as 'normal' as possible after the trapping period. Unfortunately, using our deployment strategy, there is no way of testing for any effect of trapping on associations. Data were collected at night (between sunset and tags turning off at night and tags turning on and sunrise in the morning), avoiding any disturbance of NC crows during daylight hours. During the night when tags were still pulsing, tags were monitored for time drift and encounter log levels, ensuring the day-time network was completely undisturbed.

Data cleaning

While we checked clocks on tags and basestations frequently, both devices would 'reset' and record the incorrect time in their encounter logs. These were easily identified, because logs downloaded in systematic, time-ordered sequences to basestations. Clocks discovered in the field to have 'reset' were set back to the correct time. Moreover, each tag's internal clock drifted from the real time, as there was variation in the crystal controlling the number of 'ticks' per second. During deployment, we calibrated clocks if they drifted, and subsequently during analyses, all basestation clocks were corrected to be within 3 seconds of real time. Tags' internal clocks were corrected real-time, and were within 10 seconds of the actual time throughout the study period; no *post-hoc* time correction was performed.

Association matrices

For every pair of individuals in association, each individual created an encounter record with duration of the encounter, and the maximum, minimum, and mean received power of the incoming signal. We combined the two unique logs from each tag to create a single encounter record for the tag-pair. To do this, we first filtered the dataset for encounters above a specified RSSI filter using each tags' mean recorded RSSI value for the encounter. Since each tag has a different sending and/or receiving ability (see Chapter 2), we merged the encounter record by simply choosing the maximum period of time in which at least one tag recorded an encounter at the filtered RSSI value. If there was less than or equal to a 20 second break in the encounter, the logs were further combined into a single encounter. This process allowed for only a single encounter log for each pair of NC crows. To create the association matrix of our population of NC crows, we summed the time each tag-pair spent in association for the specified period of time.

Results

Summary statistics of data

After a thorough assessment (as described above) of all tags, we removed four tags due to either significant drift (drift that impeded on daytime—between sunrise and sunset—quantitative assessment) or tag failure (the tag ceased to operate). We failed to record any data from four tags, and no data from these four failed tags were included in final analysis. Tag 21 failed on day 309 (day 11); Tag 36 on day 308 (day 10); Tag 70 on day 302 (day 4); and Tag 82 on day 305 (day 7). In addition, Tag 35 did not receive or store any received logs, but the tag transmitted throughout the time period, and as such, was included in all analyses.

To ensure tags and basestations were not memory-limited and thus, missed recording associations, we monitored the level of encounters on the on-board memory of both tags and basestations. The maximum number of logs on a tag through the deployment period (Baseline to Return-to-baseline) was 885 logs from Tag 10 on 4-NOV-2011. The maximum number of logs on a basestation through the deployment period (Baseline to Return-to-baseline) was 47208 logs on basestation 150 downloaded on 4-NOV-2011 (recorded on master message log at 21:10 on 4-NOV-2011). However, note that 58645 logs were downloaded from basestation 140 on the night of 27-OCT-2011 (recorded on master message log at 12:31 on 28-OCT-2011); this was most likely due to not clearing the basestation before deployment. Collectively, we recorded 239,075 tag-to-tag and 579,024 tag-to-basestation logs over 19 days from our fully operational tags and basestations.

Community analysis

Using the association matrices described above, I implemented four community detection algorithms in the '*igraph*' package in R (R Development Core Team): Betweeness, Spinglass, Fastgreedy, and Walktrap (Table 1). I describe these four algorithms below. The primary method used to detect communities in behavioral ecology is the Girvan-Newman betweeness algorithm (Croft *et al*. 2008); I perform three other less used, more restrictive measures of community detection to confirm results performed by the betweeness algorithm, and potentially detect smaller structures in the network topology (Newman and Girvan 2004).

Community detection algorithms rely upon a modularity score: a measure of the strength of division that a network can confidently be broken into its smaller units (often called groups, clusters, communities, cliques, etc.; *c.f.* Croft *et al*. 2008). A high modularity signifies that the network contains dense connections

within sub-groups and weak ties between communities. It is recognized that modularity has a lower limit of detection (or a limited ability to detect smaller groups within larger groups), and as such, detection algorithms often struggle to identify small sub-communities (Karrer *et al*. 2008). Herein, I use four detection algorithms, all using modularity, to identify network structure.

In addition to using network analysis to identify communities, crows were trapped from four trap sites, revealing another possible method to assign NC crow community membership. These two classifications, based upon *in silico* quantification and *in situ* methods, are compared and discussed in Table 1. There are no currently established procedures to determine which method of community detection algorithm is 'correct' or how to interpret multiple tests of community detection algorithms. Therefore, I qualitatively describe the similarities and differences between the outputs of these community detection algorithms, and use the outcome from all algorithms.

i. Betweeness (Girvan-Newman)

The Girvan-Newman betweeness algorithm measures the number of shortest paths through the graph (network) with the premise that birds within the same module will have shorter path lengths than those birds not in the same module. Removing individuals with the highest edge betweeness score, a dendrogram of the network is created assigning clusters based upon the modularity (Newman and Girvan 2004). To implement this algorithm, I used the igraph package in R using the function edge.betweenness.community().

ii. Spinglass

This function finds communities in a graph (network) consisting of many edges inside of and few edges outside of the module. Specifically, few negative edges ought to appear inside a community, and many negative edges between communities. The spinglass function solves this problem by approximately partitioning the vertices into communities through optimizing an energy function. Normally this function is used when there are different signs for weighted associations (+ and – weights); however, this function operates regardless of sign (Reichardt and Bornholdt 2006, Traag and Bruggeman 2008). For example, if I use a positive integer range to represent a range of affiliative behavior and a negative integer range to score antagonistic behavior, the data could be entered into the algorithm without the need to alter the data. To implement this algorithm, I used the igraph package in R using the function spinglass.community().

iii. Fastgreedy

This function finds dense sub-graphs (communities) by optimizing the modularity score, or determines splits in the network while maximizing the best grouping scores. This algorithm was developed to determine sub-groups in large networks, but works with small networks (as defined in Clauset *et al*. 2004). To implement this algorithm, I used the igraph package in R using the function fastgreedy.community().

iv. Walktrap

The walktrap algorithm also finds densely connected sub-graphs via random walks within the network through the premise that short random walks tend to stay in the same community (Pons and Latapy 2005). To implement this algorithm, I used the

igraph package in R using the function walktrap.community().

Community designation

Table 1 identifies each crow, and the community to which it belongs based on each of the *in silico* designations, and the location of capture. The Girvan-Newman protocol reveals two communities (See Figure 2): the Northern community and the Southern community, with bird assignments largely based upon the location of capture for each bird. Spin-glass, fast-greedy, and walk-trap algorithms revealed that the make-up of each community is different, as the Northern community is much less sub-divided than the Southern community. The Southern community breaks down into cliques, or networks in which each bird is connected to every other bird. In addition, these cliques have a significant increase in the total time spent in contact than with other birds within the same community, suggesting these birds form core social families. These results are explored below in the *Relatedness* section.

Degree and duration

Mean degree was quantified for 1) the whole population, 2) the Northern community, and 3) the Southern community; I summed the number of unique crows associating within the same specified group (see 1-3 above) each day, and divided by the number of possible crows in the network (*i.e.*, I summed the number of edges for the entire population on day 299, and divided by 33, the number of crows in the population). The unit of this calculation is 'edges/bird' (Figure 3). Across a range of distances (labeled as RSSI, a proxy for distance), more social partners than expected for a core-social family (degree of 4) were observed. At RSSI 0, or *ca.* 10 to 15

meters between birds, 6.6 ± 0.77 associations were recorded, approximately 2 birds above that expected for the largest social-family.

Mean duration was quantified for the Northern and Southern communities; I summed the time that crows were associating within the same specified group (see 1-3 above) each day, and divided by the number of possible crows that could associate (*i.e.*, I summed the time in seconds for the entire population on day 299, and divided by 33, the number of crows in the population). The unit of this calculation is 'seconds/bird' (Figure 3). Interestingly, at RSSI 0, or *ca.* 10 to 15 meters between birds, 5659 ± 1685 seconds/bird were recorded, suggesting associations were not limited to a few seconds at short distances between non-family birds.

Sexing and Relatedness

First-order relatedness was determined using previously established techniques (See Rutz *et al*. 2012b), and the full genetic network of all crows tested to date is presented in Figure 4. There is no genetic structure to community assignment, suggesting that juvenile dispersal occurs between sites (Figure 4). Additionally, we uncovered two triad families with adult males that spent equivalent time with a juvenile (offspring) as the first-order related adult female, yet these adult males were not first-order related to the juvenile.

Discussion

We successfully deployed a new proximity system on wild NC crows, collecting over 239,000 tag-to-tag logs and 579,000 tag-to-basestation logs over 19 days. In addition, data was collected for 33 of 41 NC crows, with 4 tags going missing and 4

tags failing during deployment. Overall, our tags functioned properly with the maximum number of logs on tags never exceeding 25% of the predicted limit, and basestations recording no more than 10% of their predicted maximum number of logs. While there were problems with tag resets and drifting clocks, we were able to *a posteriori* correct these errors, especially since we monitored tags *in situ*. Altogether, our system overcame limitations, such as weight and autonomous data transmission, and we successfully mapped social networks of a wild passerine bird.

Using four community detection algorithms, as well as identifying the trap site of each crow, we quantitatively described two communities, and qualitatively discussed the sub-structure consisting primarily of family units at the Southern community. While NC crows were captured at two sites at only 1200 meters apart, the clear community structure implies that these crows do not use the same space. Future studies investigating the role of space-use (measured as location in space rather than proximity between tags) driving association patterns could confirm this implication. Previous work mapping the genetic structure of this population revealed no genetic differences between two adjacent valleys (Rutz *et al*. 2012b), and herein we further demonstrated that our population contained no community-level genetic structure (See Figure 4). Qualitatively, we confirmed results presented by Holzhaider *et al*. (2011), that social family units form the first level of social structure (Hinde 1976), and was differentiated from more broad-scale community structure. Our results taken together with the outcomes from Holzhaider *et al*. (2010, 2011) and Hunt *et al*. (2012) further suggest that the social family is the core unit of the social structure in wild NC crows.

We revealed that at very close distances, there were numerous social partners (See Figure 3), contradicting the prediction by Holzhaider *et al*. (2011) that

the social network would consist of few, non-social family encounters. NC crows are extremely difficult to observe in the wild, with numerous indirect ways to measure their behavior (Rutz *et al*. 2007). One limitation of autonomous technology recording spatial associations is missing the interactions that take place when two individuals are in the same vicinity. While we were unable to concurrently measure their behavior, future studies could concurrently deploy miniature cameras and these proximity devices, capturing both the associations and interactions of wild NC crows. Currently, the combined weight of a miniature camera and our proximity device is too heavy, though with further miniaturization, improvement in battery life, and integration of multiple systems into a single deployable device, this approach will be possible.

The development of miniaturized technology has allowed for the mapping of a wild NC crows network, revealing a dynamic social structure. While some associations were weak, and many encounters are likely to have occurred in non-foraging contexts, the numerous connections widen the scope for potential information flow outside of core social families. Future work could manipulate the network to understand drivers of network topology, map their home ranges to understand ecological factors, and map the spread of information through the population. Our proximity system is suitable for a wide range of contexts, deployment on small animals, and collecting high-resolution datasets: all necessary steps to understand biological processes through network analysis in nature.

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Table 1. Five methods to determine community assignment. Each tag was assigned, first to a community based upon which trap site the bird was captured (column 1: 'Trap site'), and then was assigned a (sub-)community based on four statistical methods to determine community (Columns 2-5: 'Girvan-Newman', 'Walk-trap', 'Fast-greedy', and 'Spin-glass'. There was three trap sites: one in the center of the Northern community ('N'), one in the central of the Southern community ('S'), and one in an adjacent valley ('T' for Tabou). If more than one community was uncovered, they were numbered; any isolate (non-connected) birds were labeled 'ISO'. To visually aid clustering of groups across community-detection algorithms, each cell is colored to match a group-designation (N-yellow; S- aquamarine; T- grey; S1- orange; S2- strawberry; S3- cerulean; S4- forest green; ISO- purple).

Tag ID	Trap site	Girvan-Newman	Walk-trap	Fast-greedy	Spin-glass
10	N	N	N	N	N
11	N	N	N	N	N
19	N	N	N	N	N
22	N	N	N	N	N
29	S	S	S	S	S
32	N	N	N	N	N
35	N	N	N	N	N
38	N	N	N	N	N
40	N	N	N	N	N
42	N	N	N	N	N
47	N	N	N	N	N
49	N	N	N	N	N
54	N	N	N	N	N
56	N	N	N	N	N
58	N	N	N	N	N
59	N	N	N	N	N
61	N	N	N	N	N
66	S	S	S	S	S2
67	N	N	N	N	N
68	S	S	S1	S1	S1
71	N	N	N	N	N
72	S	S	S	S	S
73	S	S	ISO	S4	S2
74	S	S	S1	S1	S1
75	S	S	S	S	S
76	S	S	S	S	S
77	N	ISO	ISO	ISO	S3
78	N	N	N	N	N
79	S	N	S1	S1	S1
80	S	S	ISO	S4	S2
81	S	S	S1	S1	S1
84	S	S	ISO	S3	S3
85	T	S	ISO	S3	S3

Figure 1. Equipment used to map social networks in wild New Caledonian crows. (a) Tags drying after electronic parts were placed into a protective coating; **(b)** basestations ready for deployment; **(c)** Yaggi antenna connected to the computer through a program called *pimaster*; **(d)** basestations being prepared for deployment throughout the study system; **(e)** tags being prepared for deployment on our study subjects. Photos taken by study team.

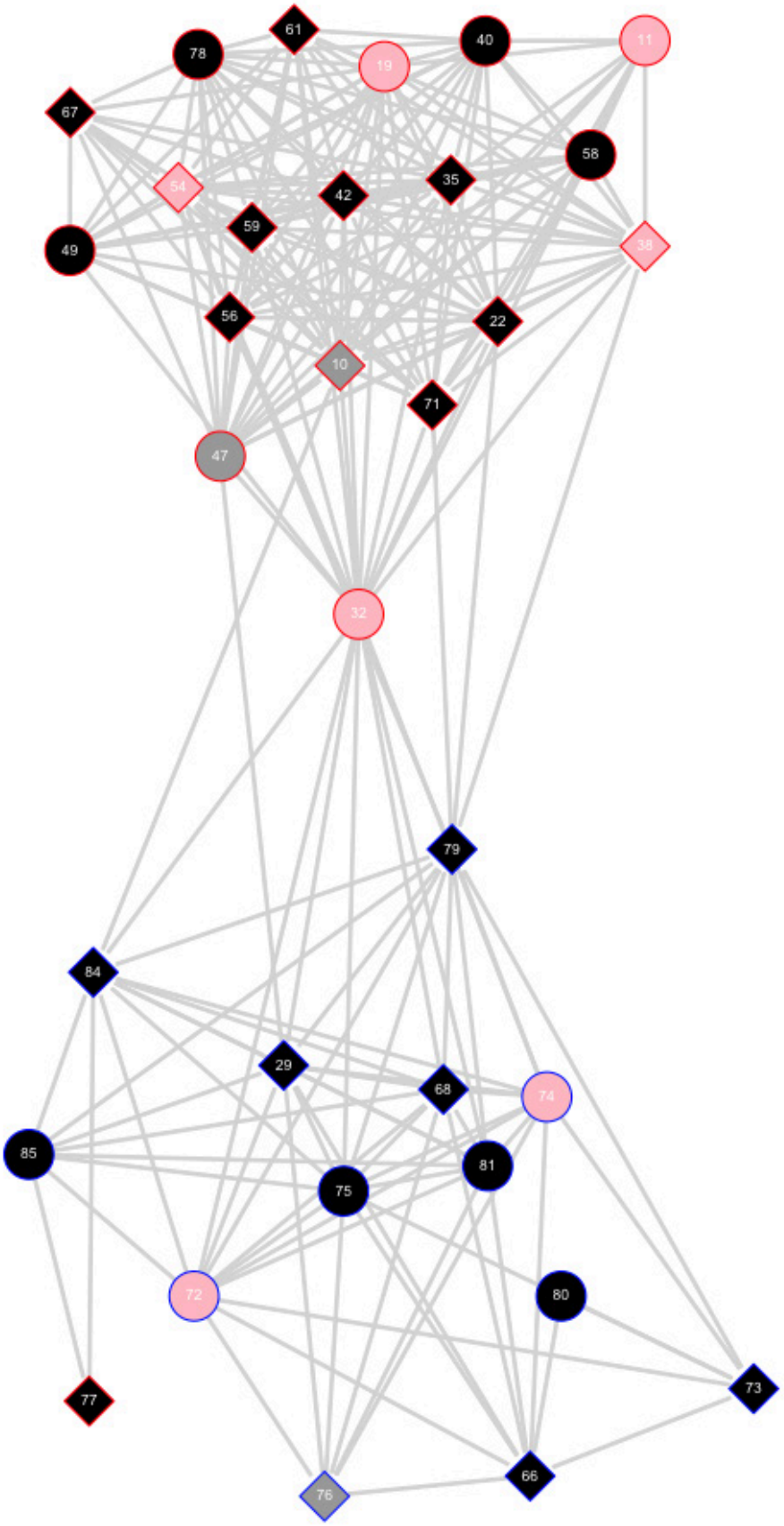
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Figure 2. Spring-embedded network based on Girvan-Newman betweeness for close-range associations. Each NC crow is identified by sex (symbol shape; male: diamond; female: circle), age (symbol color; juvenile: pink; immature: grey; adult: black), and trap site (symbol border color; Northern: red; Southern: blue, including the single bird trapped at the 'Tabou' trap site). The spring-embedded network shows the total duration spent in close association, with those spending more time in association being closer; note, some nodes were moved slightly to allow for easier view of the connections.

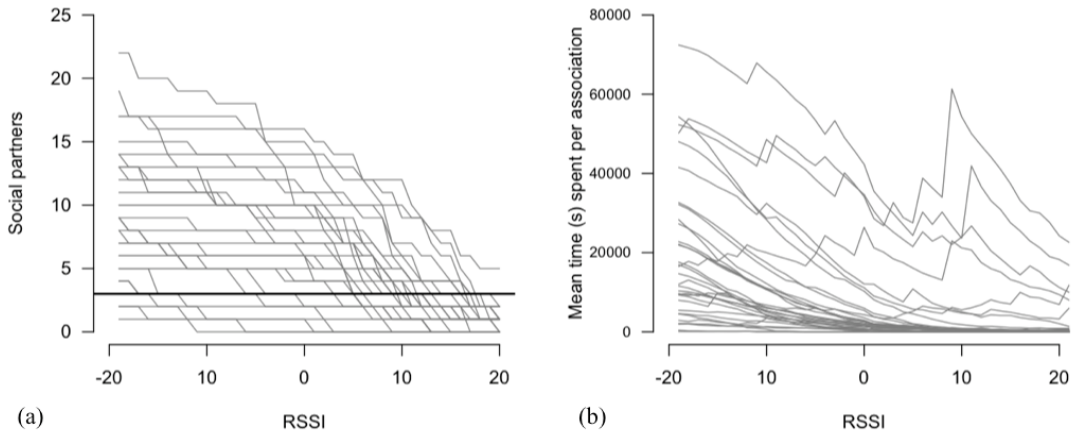

Figure 3. The number of social partners and the mean number of seconds spent per association. (a) At RSSI 0 (distances *ca.* 10-15 meters meters), NC crows have associations with more social partners (solid horizontal line) than predicted in a core family unit (6.6 ± 0.77 associations). **(b)** A substantial amount of time spent at far and close distances, with some crows spending thousands of seconds in association per bird. In addition, at RSSI 0, crows spent on average 5659 ± 1685 seconds in association.

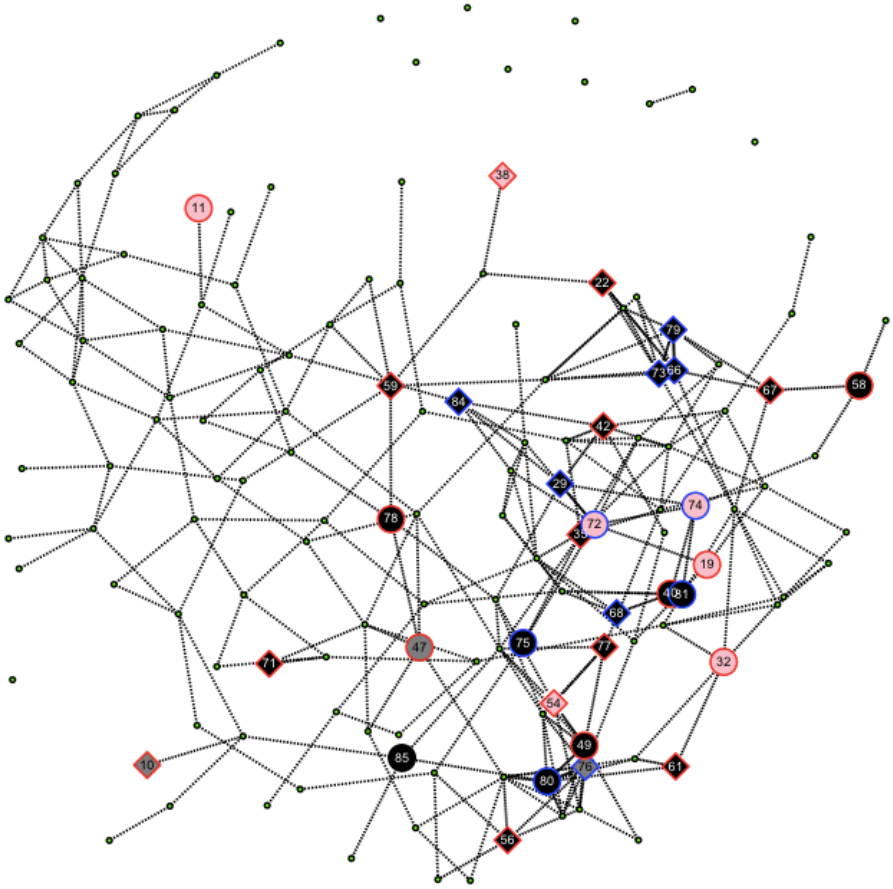

Figure 4. Network of first-order relatedness of wild NC crows. Each small circle represents a NC crow, and each line connecting these small circles represent first-order relatedness. The crows with unique identifiers represent NC crows' first-order genetic relationship. Each NC crow is identified by sex (symbol shape; male: diamond; female: circle), age (symbol color; juvenile: pink; immature: grey; adult: black), and trap site (symbol border color; Northern: red; Southern: blue, including the single bird trapped at the 'Tabou' trap site). There is no apparent genetic division due to community structure, suggesting that NC crows disperse between communities.

CHAPTER 5
MAPPING SOCIAL NETWORKS IN WILD NEW CALEDONIAN CROWS

This is a narrative chapter from part of an in prep manuscript (co-first author).

Abstract

Studies mapping the social network of wild animals have increased in recent years, especially through the advent of better devices that record associations autonomously. Yet, experimental manipulation of network topology, revealing changes to social structure, has been difficult to undertake. Here, we present the results of an experimentally placed food glut modeled after a natural tree-fall event by recording in sufficient resolution changes to network metrics. During the experimental period, we quantified an increase in social partners, time spent in association, and co-roosting pairs. Moreover, we quantified the loss of the correlation between associations and first-order relatedness during experiment 2, signifying a loss of the genetic barriers to information exchange. After removing the experiment, we witnessed some effects, such as an increased number of roosting partners, and in one community, an increased time in association, lasting for at least 5 days post-experiment. Altogether, we uncovered environmental changes that increase the potential for information exchange, suggesting that natural tree-fall events facilitate elevated oblique/horizontal information exchange.

Introduction

The social organization of wild animal populations have been investigated for well over half a century, and certain ecological factors, such as resource distribution and predation, play a role in shaping social structure, quantified by interactions and/or associations between members of a group (Hinde 1964, Alexander 1974, Rubenstein and Wrangham 1986). Many animal social structures have been characterized by fission-fusion dynamics, defined by groups frequently combining into larger assemblages and separating into smaller subgroups (Langman 1977;

Couzin 2006; Aureli et al. 2008). Fission-fusion dynamics have been suggested in numerous taxa, such as fish (Hoare *et al*. 2004; Kelley *et al*. 2011), baboons (Kummer 1968), jaguars (Schaller 1972), elk (White *et al*. 2010), elephants (Archie *et al*. 2006), and dolphins (Lusseau 2003). Environmental conditions have been suggested to be one cause fission-fusion dynamics in order to maximize benefits (*e.g.*, reproduction or foraging) and minimize costs (*e.g.*, predation; Rubenstein and Wrangham 1986).

One increasingly popular method to quantify sociality is social network analysis, which quantifies the population dynamics of animal societies (Croft, James and Krause 2008). Originating in mathematical graph theory with extensive use in human sociology (Wasserman and Faust 1994), network analysis was quite limited in ethology until the early 2000s, during which a revolution in computerized analysis spurred further use in wild animal populations (Wey *et al*. 2008). Having now been applied to numerous taxa (*c.f.* Croft, James and Krause 2008), social network analysis has quantified drivers of sociality, such as genetics and space use.

The last decade has seen an increase in our understanding of animal societies, with experimental manipulations revealing underlying structures of numerous behaviors (Flack *et al*. 2006; Claidiere *et al*. 2013). Flack *et al*. (2006) used social networks analysis to quantify changes in the network structure of pigtailed macaques to determine the underlying mechanism governing conflict management, discovering that policing maintains and stabilizes conflicts. Combining the power of social network analyses and experimental manipulation, Claidiere *et al*. (2013) mapped the spread of a learned behavior through a population of squirrel monkeys, and suggested that the acquisition of the novel foraging technique was socially mediated. Together, these studies demonstrated that

the quantification of network topology can reveal the drivers of animal behavior in response to an experiment; yet, both studies are captive studies, and neither described the actions, behaviors, and responses to an experimental apparatus in the wild.

New Caledonian crows (*Corvus moneduloides*; hereafter, NC crows) are prolific tool-users and manufacturers: crafting tools from multiple types of materials to extract hidden food items, such as beetle larvae (Hunt 1996; Hunt and Gray 2003; for a review, see Rutz and St Clair 2012). In addition, NC crows are suspected of acquiring and accumulating cultural information, passing on information related to tool properties, tool-use, and/or the steps necessary to manufacture a tool (Hunt and Gray 2003). While initially NC crows were suggested to have a small social network (Holzhaider *et al*. 2011), we demonstrated that wild NC crows have numerous social partners (Chapter 4, Rutz *et al*. 2012). While the social network has been quantified, the role of natural processes, such as the fall of a tree infested with beetle larvae, in altering the social organization of wild NC crows is unknown, and could yield significant advances in our understanding of the potential for NC crows to exchange information. Additionally, understanding the plasticity of the social structure of wild NC crows will facilitate more refined and better error assessment of future models of information exchange.

Here, to understand NC crows' response to an experimentally placed food glut, we measured network parameters, such as social partners and time spent in association, over time to demonstrate changes in the network's information exchange potential. In addition, to determine whether the network was altered away from the experiment, we measured changes to the roosting network of these NC crows. Moreover, to investigate whether relatedness correlates with social structure,

we quantified the relationship between genetics and associations each day through all experimental periods. Altogether, we sought to measure, for the first time in wild birds, changes to the NC crow network owing to an experimentally placed food glut.

General Methods

Encounternet

As described in previous chapters, *Encounternet* consists of three components: (1) animal-mounted tags; (2) basestations; and (3) 3-element Yagi antennae. Since *Encounternet* was built with custom software, all devices are capable of communicating with all other components. For detailed information, see chapter 2 or chapter 4.

Adaptive experimental design

We monitored daily association patterns and locations of each bird after each data collection (occurring every 1-2 days and always the night before a change in experimental condition as defined below). We aimed to alter the network experimentally after 7 days, which was reflective of the estimated number of days that we predicted to be the lifespan of our tags. We measured a baseline, two experimental periods, and a return-to-baseline condition. Using preliminary analyses from the baseline period, we designed an experiment to alter network topology, or the network structure, of our population of tagged birds.

We decided that the placement of a food glut, composed of logs filled with beetle larvae, could serve as a proxy for a natural tree fall event (See Figure 1), and due to the community structure (as shown in chapter 4), we aimed to draw the two

communities together into a central location. After monitoring this experiment for 3 days (with no observed recruitment to the site), we modified our experiment to be community-centric tree fall events, and monitor changes within each community (and the population as a whole) in response to the experimentally placed food-glut.

The outcome of this adaptive design was not the pre-planned division of three 7-day experimental periods, but was four conditions defined by: **baseline** (when no experimental apparatus was placed); **experiment 1** (experiment attempting to merge two communities (inter-community), as defined in chapter 4 in the baseline, described below); **experiment 2** (experiment attempting to increase within-community associations (intra-community), as defined in chapter 4); and **return-to-baseline** (experimental condition was removed from all sites). Finally, the return-to-baseline was limited in time by a bulldozer (forging a new road through our study site) entering our site after 5 full days of data collection.

Statistics

i. Network metrics

To determine changes in basic network metrics, we quantified the mean degree (number of social partners) and duration of associations in wild NC crows. To assess unique responses to the experiment by community, we grouped the data into the Northern and Southern community (see chapter 4 for details), considering only the associations within communities. We compared mean degree and duration by treatments (baseline, experiment 2, and return-to-baseline) using a Kruskal-Wallis test to determine initial significance, and then a Wilcoxon test to determine pair-wise significance (see Figure 2); alpha levels were adjusted using a Bonferroni correction, and the value is stated below when necessary. In addition, since we were

unsure whether experimental effects were sustained in the return-to-baseline, statistical tests were also re-run using a pre- and post-start of experiment 2.

ii. Roosting networks

Roosting associations were identified *post-hoc*, as all associations must have recorded durations of time spent in association between 19:30 to 20:00 at night, and between 4:00 and 4:30 the following morning. We included all durations of association as long as associations were recorded once in the evening and again in the morning at the minimum specified RSSI mean value. Roosting networks were generated for four RSSI mean values: -20, -10, 0, and 15. To test for significant differences between time periods, a Kruskal-Wallis test was used, followed by pair-wise Wilcoxon tests; statistical analysis did not include experiment 1, as no changes due to experiment 1 were observed—analysis reveals only two NC crows were recruited to the site. Experiment 1 is presented in Figure 4 for qualitative assessment. Alpha levels were adjusted accordingly with a Bonferroni correction, which is stated in the results section below. Importantly, the premise of defining roosting *a posteriori* strives to capture a specific biological assumption about roosting behaviour: NC crows have not been observed flying at night. We expected NC crows to adjust their orientation or walk along a perch for short distances. Critically, no independent verification of roosting was undertaken because we did not want to disturb the birds throughout this study period to ensure a completely undisturbed population except for data collection and planned manipulations.

iii. When does the change in associations occur?

Association logs were aggregated into one-minute bins, summed by the frequency of associations that occurred at the specified time. The maximum number of associations to occur during each day was identified, and a Kruskal-Wallis test comparing experimental conditions (baseline, experiment 2, and return-to-baseline) was undertaken. The time of elevated associations was also documented.

iv. First-order relatedness correlates with associations

We quantified whether the genetic matrix (1st order relatedness) is correlated with each daily association matrix, and to determine whether the correlation changes were different between experimental conditions. The genetic matrix consisted of binary values (0 and 1) with 1 signifying first-order related. The association matrix is a continuous matrix, with pair-wise encounters designated with the number of seconds in association. All data is RSSI mean greater than or equal to 15. Matrices were created for each day, each daily matrix was compared to the genetic matrix, and to control for community structure, I performed a 'constrained randomization' for membership in the Northern or Southern community. I used the mantel() function in the 'vegan' package in R (R Development Core Team 2014), which performs a Mantel test between the two matrices using 10000 permutations.

There are two common ways to perform randomization tests with data not collected using the gambit-of-the-group (see chapter 4 for description): Node-label permutation and edge rearrangement (*c.f.* Croft *et al*. 2011). A key factor in choosing between these two methods is the confidence in the edges, or measured value between individuals; Since we are extremely confident of our edges (and non-

edges), alongside our null hypothesis resembling the fact that any individual could occupy any network position, we performed a node-label permutation.

Results

To explore the changes to network topology due to experiment 2, we quantified five key measures of network organization: 1) mean degree, 2) mean duration, 3) daily roosting associations, 4) time of network topology changes, and 5) correlation of associations with genetic relatedness.

Network metric changes

The population of NC crows had a significant increase in the mean degree (connectedness) during experiment 2, though this was driven solely by changes in the Northern community (**Population**: $\chi^2 = 11.2$, df = 3, p = 0.011; **Northern**: $\chi^2 = 11.2$, df = 3, p = 0.011; **Southern**: $\chi^2 = 4.7$, df = 3, p = 0.20). Pairwise testing in the Northern community revealed a trend with a Bonferroni-adjusted alpha ($\alpha = 0.007$) between the baseline and experiment 2 (W = 0, p = 0.01), and between experiment 2 and return-to-baseline (W = 0, p = 0.02). Altogether, experiment 2 trended towards increasing the number of social partners relative to baseline conditions, and the number of partners did not remain elevated after the experiment was removed.

The population of NC crows had a significant increase in the mean duration of associations during experiment 2, again driven solely by changes in the Northern community, while the Southern community trended towards an increase in the mean duration (**Population**: $\chi^2 = 10.0$, df = 3, p = 0.019; **Northern**: $\chi^2 = 8.8$, df = 3, p = 0.033; **Southern**: $\chi^2 = 7.3$, df = 3, p = 0.063). Pairwise testing in the Northern community revealed non-significant differences with a Bonferroni-adjusted alpha (**α**

= 0.007) between the baseline and experiment 2 (W = 0, p = 0.01), and between experiment 2 and return-to-baseline (W = 0, p = 0.02). While these pairwise tests were non-significant using the most conservative alpha correction factor, we observed a trend in the increase in mean duration during experiment 2 within the Northern community.

However, since we do not know the best grouping of our data *a priori* because effects could potentially continue even after an experiment is removed, another approach to statistically assess this population is to divide pre- and post-experiment 2. The population of NC crows had a significant increase in the mean duration during experiment 2, and this was driven by changes in the Southern community with the Northern community having a trend towards an increase in the mean duration (**Population**: W = 7, p = 0.001; **Northern**: W = 21, p = 0.05; **Southern**: W = 12, p = 0.006). Grouping data by pre- and post-experiment 2 did not alter the outcome of mean degree (**Population**: W = 12, p = 0.008; **Northern**: W = 11.5, p = 0.007; **Southern**: W = 35.5, p = 0.43), suggesting the Southern community did not respond to changes to the mean number of associations per bird (however, see chapter 8 for a robustness analysis). Interestingly, breaking down the data by age revealed that the juvenile-adult associations were possibly driving the lack of returning to baseline, but the sample size is insufficient for statistical analysis.

Roosting networks

For RSSI -20, -10 and 0, a Kruskal-Wallis test revealed a significant effect of experimental condition on association quantities (see Table 1 and Figure 4 below). Altogether, associations were significantly increased in experiment 2 and return-to-

baseline compared to the baseline; experiment 2 and the return-to-baseline periods were not significantly different. This significance was maintained through RSSI values greater than or equal to 0; however, significance was lost at RSSI values greater than or equal to 15. These data suggest that the increase in roosting associations due to the experiment was not generated at extremely close distances but was generated by associations at intermediate distances (*ca.* 10-20 meters). Independent assessment of roosting locations measured by proximity to each basestation revealed no change in the base station near each bird's roosting location (data not shown). Therefore, an increase in density of roosting within their normal roosting location was observed.

When does the change in associations occur?

We uncovered a sharp increase of associations during the morning period of experiment 2 immediately after sunrise, between 5:00 and 6:00am (See Figure 3). Additionally, we found a significant difference between the baseline, experiment 2, and return-to-baseline conditions ($\chi^2 = 7.84$, df = 2, $p = 0.019$). To isolate the statistical effect, we ran *post hoc* Wilcoxon tests, and adjusted our alpha value using a Bonferroni adjustment ($\alpha = 0.017$) to correct for three additional tests. We discovered that experiment 2 had a significantly greater number of associations than during the baseline between 5:00 and 6:00am ($W = 1$, $p = 0.016$), yet only statistically trended towards having more associations than the return-to-baseline ($W = 1$, $p = 0.034$). We believe with a longer return-to-baseline period, significance would have been reached because the data suggests that a return to baseline occurred on the final two days of the experimental protocol.

Correlation of genetic relatedness

To determine whether genetics is correlated with associations, we developed two independent matrices: time spent in association each day were summed and compared with a first-order binary genetic matrix. We revealed a significant correlation between first-order relatedness and associations during the baseline, experiment 1, and return-to-baseline; yet, surprisingly, a non-significant correlation during two days of experiment 2 (see Figure 5).

Discussion

We revealed changes to basic network structure due to an experimentally placed food glut, showing increases in mean degree in the Nouthern community, and mean duration for both communities. Specifically, in the Northern community, we measured an increase in mean duration only during the experimental time period, whereas in the Southern community, the changes to duration were sustained through the return-to-baseline period. Roosting networks increased during the experimental period, and also remained elevated through the return-to-baseline period. Interestingly, NC crows did not travel to another basestation, but moved closer in the same general region. In addition, we found that first-order relatedness is correlated with associations during the baseline, but the correlation disappears during experiment 2, and then returns during the return-to-baseline: this non-significant correlation showed that the genetic structure of the network is no longer a significant determinant of associations during a treefall event. Finally, we revealed that the sharp increase in associations during experiment 2 occurred in the morning, and after the experiment was removed, NC crows quickly returned to normal morning association levels (as shown in the return-to-baseline).

Encoutnernet tags recorded the timing of changes in associations throughout the study period, revealing a sharp increase in associations in the morning, and no observable differences in associations at other times. In addition, after the removal of our experiment, we found that the sharp increase in associations quickly reduced, and the pattern of associations appeared to return to pre-baseline levels. We were unable to detect a change in the time of associations between the baseline, and experiment 2, or the baseline to the return-to-baseline; therefore, we were unable to provide additional evidence to support the 'early bird gets the worm' hypothesis, or that competition in arrival time is necessary to have the greatest probability of foraging success. Interestingly, a recent study has provided the first evidence for this hypothesis in passerine birds, though lacked the necessary high-resolution data of the population to exclude all alternative hypotheses (Farine and Lang 2013), such as the resolution of the technology was not high enough resolved to test for changes within minutes. Future work should continue to explore the 'early bird gets the worm' hypothesis to determine whether we are able to measure at high-resolution foraging competition in the wild.

A key future challenge for future wild manipulations will be replicating experiments. While we were only able to run a single experiment, we were able to monitor whether the population returned to pre-experimental conditions, and determine the length of time for experimental effects to dissipate. Importantly, two of our parameters did not return to normal after 5 full days post-experiment: the time spent in association in the Southern community and roosting networks. These results suggest that at minimum more than 5 days would be necessary before running a replicate experiment (or that the return-to-baseline must be studied before replicating). Furthermore, since roosting networks did not return back to normal,

recording associations away from experimental sites is essential, and has not been undertaken in recent studies. For example, a recent study revealed that social associations predict the discovery of foraging patches; yet, this study did not record associations that occurred outside of foraging locations (Aplin *et al*. 2012). As a consequence, this study predicted the discovery of foraging patches by associations at foraging sites; the outcome predicts foraging patch locations based upon sociality only at foraging locations instead of sociality occurring independent of a single location or situation. In addition, this study performed multiple experiments with no ability to detect changes to the network outside of these foraging locations. More generally, studies using RFID/PIT tags only record associations at foraging locations and, thus, are unable to record all associations between birds. We highly recommend studies consider these limitations when choosing an animal-borne device to measure the response to experimental conditions in the wild.

We presented the first manipulation of a wild social network and measurement of network changes at and away from the experiment. A previous captive study tracked changes to network topology through direct observation, but the results were restricted only to the captive group and may not necessarily reflect wild populations (Flack *et al*. 2006). Nonetheless, this study provided the first evidence to suggest that the use of social network analysis may provide quantitative outcomes to experiments in wild animal populations (Flack *et al*. 2006). Here, we build from this captive experiment's premise and recognize additional constraints with wild animals, such as identifying the length of time necessary to wait between experiments to ensure experiments are independent from one another.

Importantly, a key limitation of our study is that we currently lack the natural measurement of tree-fall events to relate the magnitude of our changes to

those that occur in nature. Future work to quantify tree-fall events that occur naturally will yield data to 'parameterize' our data, allowing insight from this experiment towards naturally occurring scenarios. Connecting experimental changes to wild scenarios will facilitate better models to understand the behavioral plasticity of animals' response to changes in their network topology.

Altogether, we quantified the network changes of tool-using NC crows' in response to a food glut. Moreover, we measured changes in network topology in response to the food glut, and quantified changes in sociality away from the food glut, suggesting that both are necessary for future work seeking to experimentally manipulate a wild animal social network. Futhermore, we measured a change in the correlation between first-order relatedness and associations—a first in experimentation of wild animal populations. In addition, we provided the first evidence of interdependence in experimental conditions in the wild, suggesting real-world analyses are necessary to monitor when a network returns to pre-experimental levels through multiple measures. The results presented provide the first data to implement a network-based diffusion model of information in a wild NC crow population.

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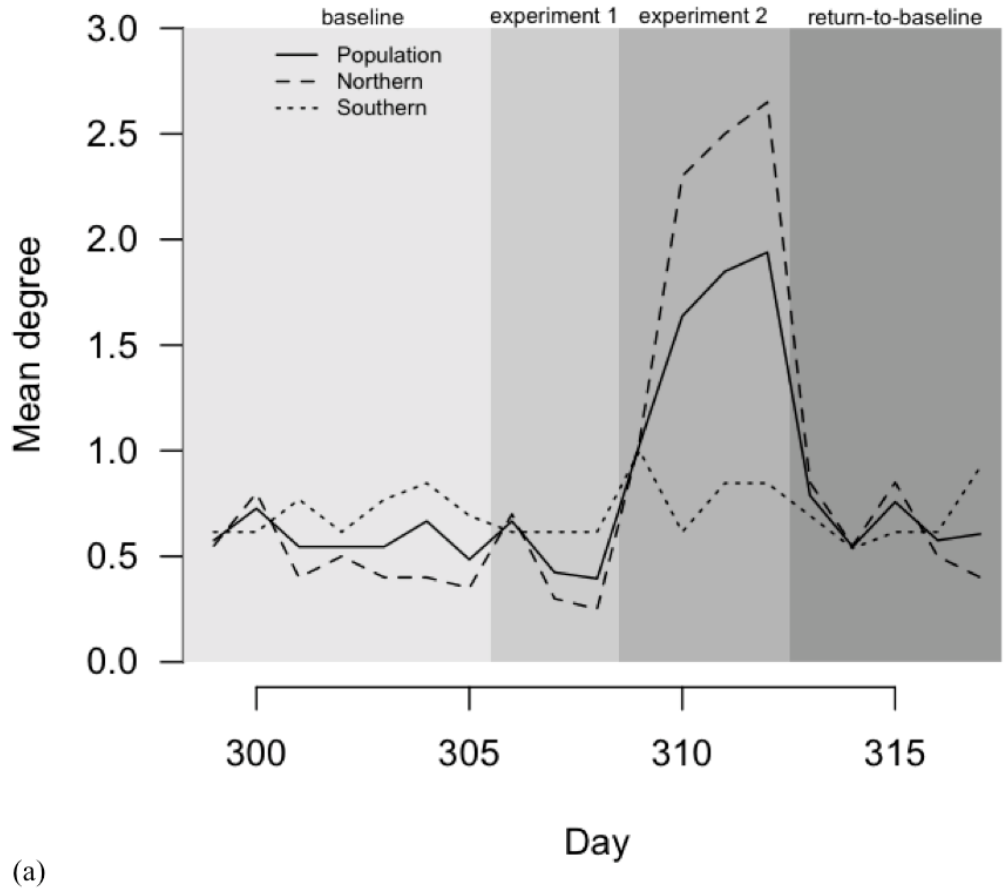
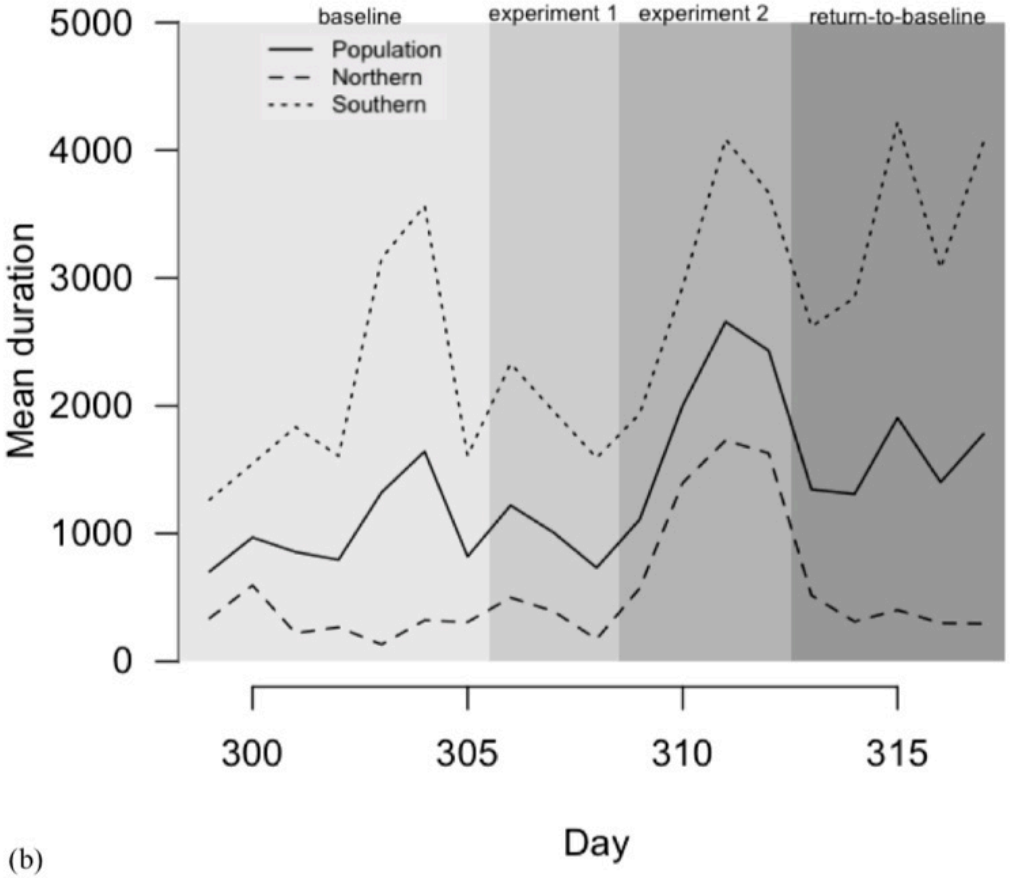
Table 1. Significance (p-) values for specified RSSI values comparing the number of roosting partners during each experimental time period. RSSI – received signal strength indicator (a proxy measure for distance); **B-** baseline (undisturbed network); **E1** – experiment 1 (inter-community experimentally placed food glut); **E2** – experiment 2 (intra-community experimentally placed food glut); **RB** – return-to-baseline (experiment 2 removed). A Kruskal-Wallis test was used to test for significance with all conditions, and a Wilcoxon test was used to determine significance of each individual pairwise comparison. Alpha was corrected using a Bonferoni correction (4 statistical tests) and was equal to 0.0125. Listed in the table are p-values with significant values' cell highlighted yellow, and values between 0.0125 and 0.025 were assigned as trending highlighted in orange.

RSSI	All conditions	B-E2	B-RB	E2-RB
-20	0.005	0.006	0.006	0.7
-10	0.006	0.02	0.01	0.5
0	0.01	0.03	0.01	0.9
15	0.5	0.5	1	0.5

Figure 1. Cerembycit beetle larvae infested trees being loaded into the back of a truck to be transported after nightfall to an experimental site.


baseline
experiment 1
experiment 2
return-to-baseline
Population
Northern
Southern
Mean degree
3.0
2.5
2.0
1.5
1.0
0.5
0.0
300
305
310
315
Day

(a)


baseline
experiment 1
experiment 2
return-to-baseline
Population
Northern
Southern
Mean duration
5000
4000
3000
2000
1000
0
300
305
310
315
Day

(b)

Figure 2. Mean degree and mean duration plots grouped by population and divided by experimental condition for 33 wild NC crows. Experimental conditions consisted of baseline (undisturbed period), experiment 1 (inter-community tree-fall event), experiment 2 (intra-community tree-fall event), and a return-to-baseline (intra-community tree-fall event removed), respectively. Mean degree is the number of associations per day divided by the number of birds within the designated population (**Population** = 33; **Northern** = 20; **Southern** = 13). **(a)** Mean degree significantly increased during experiment 2 only in the Northern community. **(b)** Mean duration significantly increased during experiment 2 in the Northern community, and the mean duration was significantly increased between pre- and post-start of experiment 2. Altogether, experiment 2 elicited changes in the network topology of wild NC crows, increasing the mean number of social partners and/or the time spent in association.

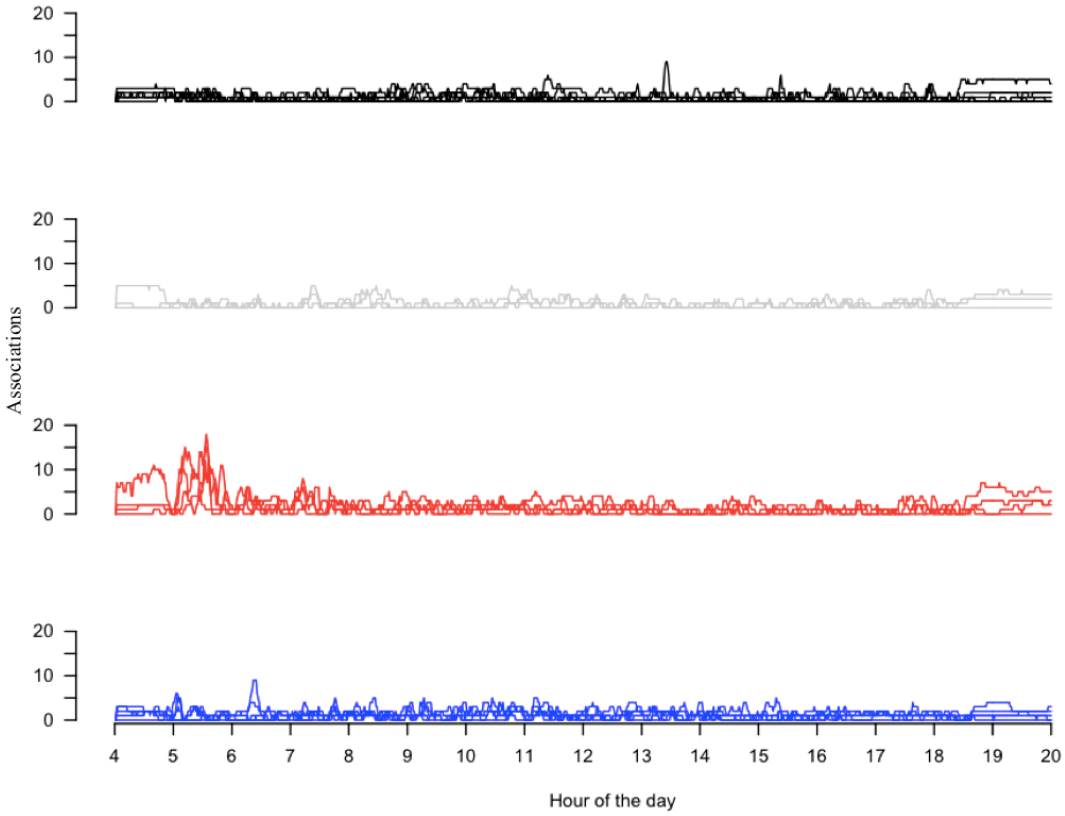


Figure 3. The number of associations occurring each minute grouped by experimental condition. Within day patterns reveal that an increase in associations occurs in the morning between 5:00 and 6:00 during experiment 2 (red) compared to all other time periods (black = baseline; grey = experiment 1; blue = return-to-baseline); Statistically, we compared the peak in the number of associations between 5:00 and 6:00 between the baseline, experiment 2, and return-to-baseline conditions (χ^2 = 7.84, df = 2, p = 0.019), revealing an increase only during experiment 2 (corrected alpha level: α = 0.017; baseline vs. experiment 2: W = 1, p = 0.016; experiment 2 vs. return-to-baseline: W = 1, p = 0.034). We found no observable differences in experiment 1.

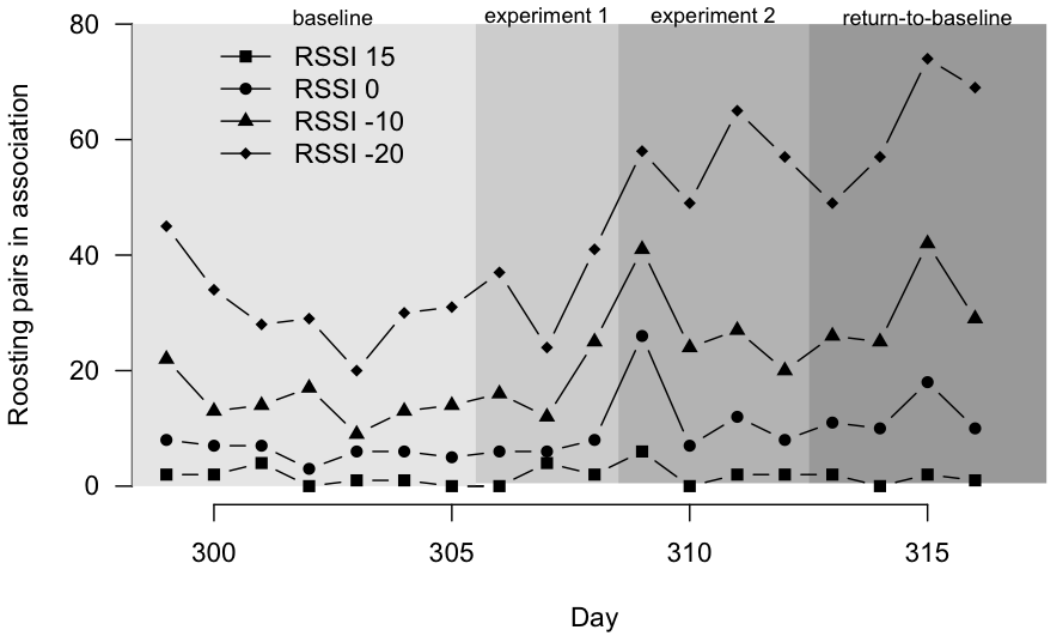
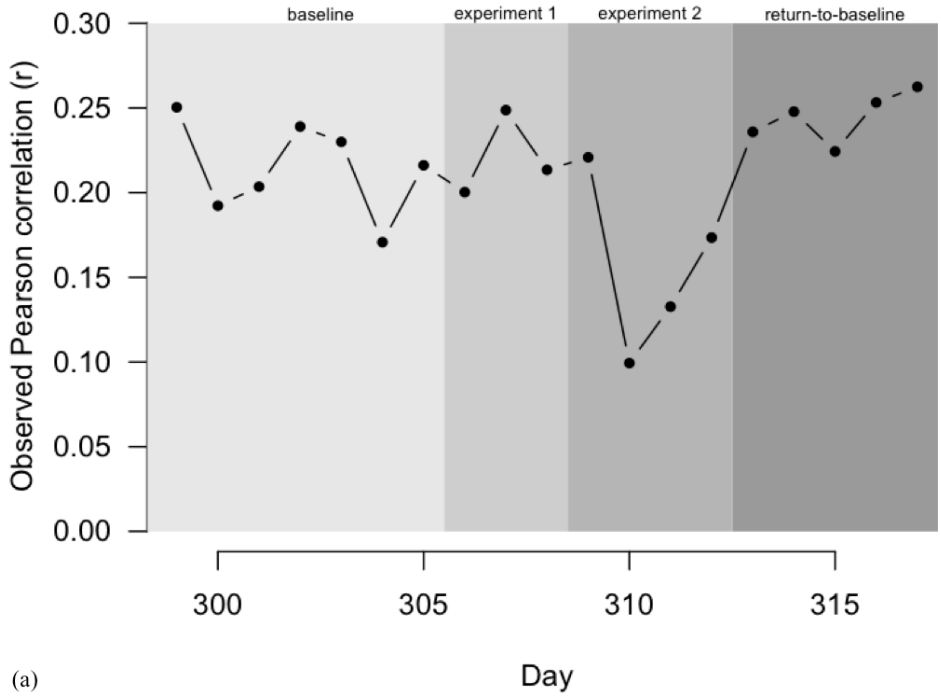
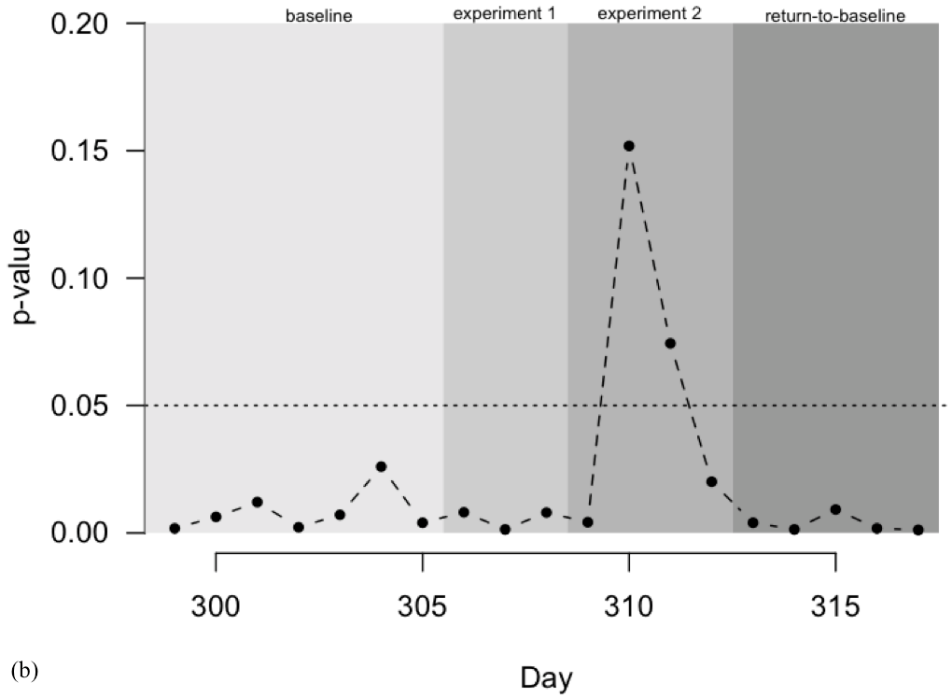


Figure 4. The number of roosting pairs each night for 18 days. Roosting was defined as being within contact at night and in the morning for the specified RSSI value. A significant increase in roosting associations occurred between experiment 1 and experiment 2, and this increase was maintained through the return-to-baseline period.



(a)



(b)

Figure 5. The correlation and significance between associations and first-order relatedness per day. (a) Correlated is an association matrix by day with a binary genetic matrix constrained by community membership. During experiment 2, the genetic correlation dropped, and the significance **(b)** was lost for the middle two days.

CHAPTER 6

A PRIORI FILTERING OF DATA FROM PROXIMITY DEVICES MISSES SIGNIFICANT BIOLOGICAL OUTCOMES (TABLE OF CONTENTS) ...145

Manuscript prepared for submission to the *Journal of Animal Biotelemetry*.

Commentary

A priori filtering of data from proximity devices misses key biological outcomes

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Running head: *post hoc* filtering ensures correct conclusion

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Abstract

Proximity devices have become a useful tool to collect detailed association data in wild animals. Using radio waves to communicate between tags, proximity devices require both a conversion of the received power into a distance and an understanding of the variation at each distance caused by extrinsic factors to produce biologically meaningful association networks. Currently, two strategies to deploy proximity devices are used: 1) setting a minimum received power before deployment to record only associations with a high enough received power, and 2) recording all possible encounters regardless of their received power, and subsequently filter data by their received power. Here, I compare these two strategies by analyzing a data set that collected all possible encounters through two experimental conditions, and I demonstrate that *a priori* filtering of this dataset can miss associations, leading to a misinterpretation of the social structure, and thus, stating incorrect biological outcomes. Future deployments of proximity devices utilizing *a priori* filtering must record encounters at a power level that is robust enough to consider the variation induced by external factors, inferring that *a priori* filtering of encounters ought to be replaced or supplemented by *a posteriori* analytical methods.

Keywords

Biologging, Biotechnology, *Corvus moneduloides*, *enCounter*, *Encounternet*, New Caledonian crow, Power, Proximity logger, Received signal strength indicator, RSSI

Main text

Collecting association data through animal-mounted technology is a vital tool to study wild animal behavior [1, 2]. For over 10 years, proximity devices have been deployed, especially on small and difficult-to-observe fauna [3], enabling the characterization of fine-scale social structures. Assessment of social networks derived from proximity data have revealed inter- and intra-specific association patterns [4], predator-prey dynamics [5], disease transmission [6], and the potential for information exchange [3]. Using radio waves to transmit animal specific data, proximity devices quantify spatial associations by converting received power to distance. Significantly, the primary deployment strategy utilized to date, with few exceptions [3], sets a minimum power *a priori* that is necessary to record an association. Relying on this strategy, studies could miss associations, leading to an incorrect mapping of the social structure, and thus, revealing incorrect biological conclusions.

Proximity systems consist of a minimum of two tags, each deployed on an animal, and necessitate receiving a signal from one-another to record an encounter [7]. The signal contains date-, time-, and ID-encoded information, alongside the power of the received signal, also known as the 'received signal strength indicator' (RSSI) [3]. Theoretically, the signal's power attenuates logarithmically through space, eventually being un-receivable at distance [8]. In a 'perfect' world, the power received at each distance would be unique. In the 'real' world, environmental factors differentially attenuate the signal, causing variation of the received power at each distance, and shortening the distance of signal reception [5, 8-10]. Variation is introduced in the received power at each distance by environmental factors (*e.g.*, height, habitat, etc.), deployment strategy (*e.g.*, placement of the tag on the animal),

and behavior of the animal (*e.g.*, changes to relative antenna orientation due to movement) [8]. Additionally, recent work has demonstrated power differences between tags, revealing another source of error that must be quantified [8, 11-13]. Altogether, error in proximity devices is substantial and must be considered to effect the interpretation of the biological outcome.

Variation in the received signal power is the fundamental factor in determining deployment strategy of the tag on the animal. Currently, two methods exist to deploy proximity devices: (1) *a priori* programming of the tag necessitating a certain power to be received to record an encounter (*e.g.*, *enCounter*), and (2) *post hoc* assessment of the power after receiving all possible pulses (*e.g.*, *Encounternet*) [8, 14]. Both strategies rely on the conversion of received power to distance, yielding associations within a specified distance to assess pre-specified biological objectives. To date, most studies use *a priori* filtering (*e.g.*, [4-6]), with only a few studies assessing received power variation *a posteriori* [3, 14, 15]. While studies using *a priori* filtering seek to mitigate and quantify missed associations by calibrating and validating received power at a specified distance [11], the impact of this decision is best assessed through *a posteriori* methods. This influence is especially true when attempting to understand complex behavior of wild animals, interacting in and moving through a heterogeneous environment.

Through *a posteriori* filtering using three levels of power to construct networks, I show that different levels of received power reveal similar biological outcomes during experimental time period 2 at site 1 (See figure 1; also see [15]). Importantly, the difference between any two consecutively measured power levels (RSSI 15 and RSSI 10, and RSSI 10 and RSSI 5) is within environmentally induced variation of received power at the higher RSSI value's distance (see [8]), suggesting

that these measured powers are statistically un-differentiable. If I used the highest of the depicted received powers (RSSI 15) through a technology that used *a priori* filtering, the increase in associations during experiment 2 would have been missed at site 2 (See Figure 1). This outcome would require a biological explanation describing New Caledonian crows (*Corvus moneduloides*) aggregating at an energy rich food source in the Northern community, but not recruiting to another foraging opportunity in the Southern community. Ultimately, I believe there is no difference in the biological outcome between the two communities; rather, the environmental factors at each site differ, and thus, the attenuation of the signal is unique for each site with the Southern community having more signal attenuation than the Northern community.

A priori filtering of received power as the primary strategy to record wild animal associations must be re-considered. Recording encounters at a greater distance than the focal distance, alongside a calibration to understand the conversion and variation of received power at different distances, allow for the assessment of potentially missed associations. This assessment is an essential step to confirm that any measured association difference is biologically meaningful, rather than a methodological artefact. While there are advantages to using *a priori* filtering, such as increasing battery life and available memory due to fewer pulses received, these benefits, in my view, will never outweigh the impact of missing key biological outcomes and misinterpreting data. Thus, setting *a priori* power levels to record associations in proximity devices ought to be robust enough to consider the variation induced by external factors, implying that *a priori* filtering of encounters should either be replaced by *post hoc* methods or programmed to allow for *a posteriori* sensitivity analyses.

Abbreviations

RSSI: received signal strength indicator

Competing interests

The author declares that he has no competing interests.

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Endnotes

None

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15. Chapter 4 and Chapter 5.

Illustrations and figures

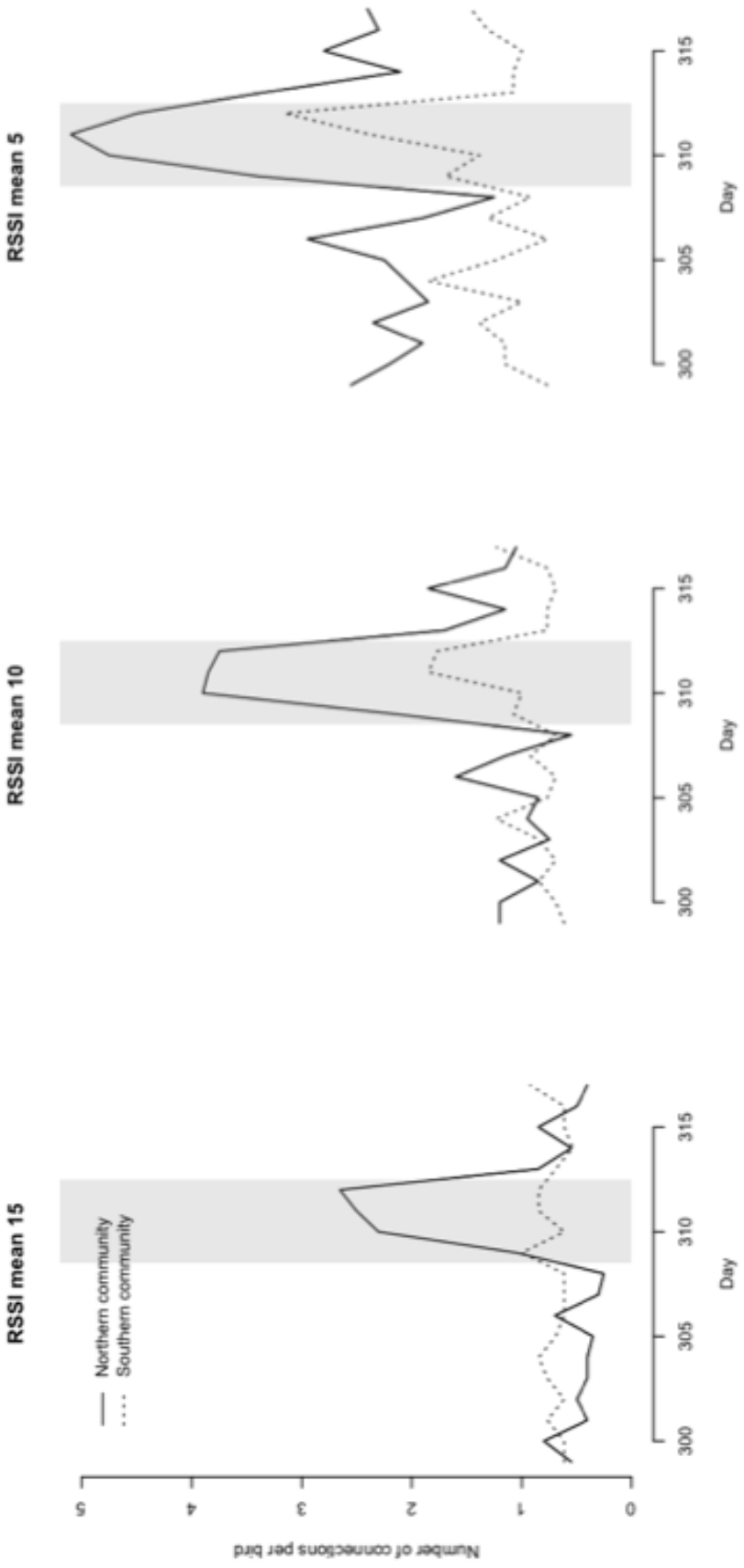

Figure 1. An example demonstrating that *a priori* filtering of data from proximity devices can miss a key biological outcome. Associations were quantified using three unique RSSI filters by day across four different treatments at two unique sites: (1) an undisturbed baseline (days 299 to 305); (2) experiment 1 (days 306 to 308); (3) experiment 2 (days 309 to 312); and (4) an undisturbed baseline (days 313 to 317). Experiment 2 is highlighted in grey. The difference between an RSSI 15 and an RSSI 10, and between RSSI 10 and RSSI 5, is within plausible environmentally induced variation of received power (see [8]). Thus, there is no statistical ability to differentiate between a RSSI 15 and a RSSI 10, as well as between RSSI 10 and RSSI 5. **(a)** A high power (RSSI 15) filter representing the closest spatial associations reveals a response in community 1 (solid line), but not in community 2 (dotted line). **(b)** A medium power filter (RSSI 10) highlights that a difference in 'community 2' is plausible during experiment 2, and the change in community 1 remains. **(c)** Furthermore, the lowest power (RSSI 5) reveals a change at community 2 during experiment 2, and retains the change in community 1. A deployment strategy filtering data at RSSI 15 before deployment would have suggested different biological outcomes during experiment 2 within each community. Yet, there is no difference in biological outcome, with the discrepancy originating in the ability to quantify associations within a heterogeneous environment, as depicted by slightly lower RSSI values.

Tables and captions

None

Preparing additional files

None

CHAPTER 7

WILD NEW CALEDONIAN CROWS USE INSERTED ABANDONED TOOLS TO INFORM FORAGING DECISIONS (TABLE OF CONTENTS) 155

Manuscript prepared for submission to *Proceedings of the Royal Society B*

Wild New Caledonian crows *Corvus moneduloides* use inserted abandoned tools to inform foraging decisions

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Short title: Abandoned tools as information

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Keywords: artifacts, cerambycit beetle larvae, culture, extractive foraging, indirect information exchange, social learning, tool adoption, tool use

Abstract

New Caledonian crows (NC crows; *Corvus moneduloides*) use three types of tools to extract hidden prey: non-hooked stick tools, hooked stick tools, and Pandanus (*Pandanus spp*.) tools. Sometimes after foraging, NC crows discard their tools in and around foraging locations, and subsequently, conspecifics have been observed using abandoned non-hooked stick tools. The significance of these abandoned tools, and the information gained from using these abandoned tools have been largely unexplored. Herein, we show that wild, free-ranging NC crows preferentially adopt previously inserted tools over tools resting on a foraging location. We demonstrate that the ease of picking up a tool does not cause NC crows' preference, suggesting the previous deployment of the tool, including its insertion, explains this preference. Sawdust, an environmental cue produced by hidden wood-boring beetle larvae, added to the location of the resting stick removed the strong preference for the inserted stick, highlighting that foraging decisions in wild, free ranging NC crows are informed by both abandoned tools and environmental cues. The preferential use of inserted abandoned tools suggests that tool characteristics, extractive foraging locations, and deployment strategies of conspecifics are passed between NC crows. Acquiring information from non-related individuals through abandoned tools increases the rate that novel foraging behaviors spread in the wild, and could be a necessary process in juvenile acquisition of tool-oriented behavior.

Introduction

An optimally foraging animal collects sufficient information to make the most informed decision regarding where and for how long to feed (see [1]). To evaluate the profitability of a location, an animal gathers personal information by observing

and even experiencing a foraging patch, or social information by observing other individuals or their products within or around a foraging patch. Collecting information from other individuals based on their actions and products, leads to social learning if, and only if, the animal adapts its behavior after acquiring this information. A unique subset of social information, potentially leading to social learning, occurs when an animal encounters products left behind by another individual without direct observation of this individual [2-7]. The quantity and quality of information gathered from these products is essential to understand the role of non-direct processes in the maintenance and spread of novel foraging behaviors.

Learning from the products of other individuals has been primarily researched in black rats (*Rattus rattus*; [2,3]) and tits (*Parus spp.*; [4-7]). Nearly all black rats reared by a knowledgeable, proficient pinecone-stripping mother acquired the most efficient method to remove scales from pinecones to retrieve seeds, whereas those reared without demonstration rarely performed the technique. When a different population of naïve rats was exposed to partially stripped pinecones in the absence of a demonstrator, over 70% of rats learned the most efficient method [3]. Similarly, chickadees (*Parus atricapillus*) previously unable to open a tub were able to remove the lid after being exposed to a partially open tub without direct conspecific observation [5]. Both findings demonstrate that products of conspecifics are sufficient to facilitate foraging behaviors. Yet, in black rats stripping pinecones, the proportion of the population that acquired the proficient methodology due to cues left by conspecifics is smaller than that of direct conspecific observation. It remains unknown if the difficulty of the foraging task determines whether trial-and-

error learning, products left by conspecifics, and/or direct observation, are necessary to solve a potential foraging task.

Tool-using species provide another opportunity to investigate the transmission, use, and significance of abandoned objects [8]. The re-use of abandoned tools has been recorded in numerous animals, including great apes (Sumatran orangutans *Pongo abelii* [9], bonobos *Pan paniscus* [10], chimpanzees *Pan troglodytes* [11-15]), monkeys (bearded capuchins *Cebus libidinosus* [16] and lion-tailed macaques *Macaca silenus* [17]), and birds (woodpecker finches *Cactospiza pallida* [18] and New Caledonian (NC) crows *Corvus moneduloides* [19-21]). The significance, quantity, and quality of information contained within these abandoned tools and their deployment are unknown.

NC crows are prolific tool users, exhibiting a repertoire of several complex manufacturing processes using multiple types of materials [19] (for a review see [22]). To forage for hidden prey, NC crows manufacture and use pandanus (*Pandanus spp.*) tools and hooked stick tools, as well as use non-hooked stick tools with little or no modification [19,21]. NC crows abandon all three types of tools in and around foraging locations with pandanus tools being left inserted into *Pandanus spp*. crowns containing out-of-reach invertebrates ([19]; C. Rutz and J.J.H. St Clair unpublished data; personal observation), hooked stick tools being left inserted into living and dead wood [19,23], and non-hooked stick tools being abandoned in and around holes containing out-of-reach cerambycit beetle larvae [21,24]. Yet, any preferential use of abandoned tools remains unexplored.

Herein, to determine whether NC crows prefer tools left behind by conspecifics, we experimentally compared NC crow preference of either inserted abandoned stick or sticks resting on a foraging location. Next, to examine

whether the stick's vertical placement or insertion drives the crows' preference, we presented NC crows a choice between an inserted stick and a vertically presented stick. In addition, to investigate whether environmental cues could alter this preference, we re-presented our initial condition with the addition of sawdust, an environmental cue signalling potential hidden prey, to the stick resting on the foraging location. We aimed to understand whether abandoned tools, which could facilitate the acquisition of stick-tool use to extract beetle larvae, inform the foraging decisions of wild NC crows.

Material and Methods

(a) Study sites and subjects

NC crows inhabit two islands of New Caledonia, Grande Terre and Maré. Our research focused on the central west coast of Grande Terre, spanning *ca.* 15 km, and encompassing three different habitats. Research was undertaken at two sites in our long-term dry forest study area (See figure 1c, sites 1 and 2; also see [21], described therein as 'Tabou and Taro Valleys'), three unique farmland sites (figure 1c, sites 3, 4, and 5), and a human disturbed site near the beach (figure 1c, site 6). Unique sites, or primary locations, were defined as being at least 1000 m from all other locations, exceeding the maximum-recorded radius of *ca.* 700 m of NC crow home ranges [20]. Since 2005, a substantial proportion of the NC crow population in our long-term study site have been individually marked using wing tags and color rings [21,25]. A large proportion of the NC crow population at the human-occupied beach location, site 6, and one farmland site, site 5, was individually marked in 2012. This investigation used only non-hooked stick tools (twigs and leaf petioles), though all studied populations have recently been observed manufacturing hooked stick tools

(See [23] and C. Rutz, J.J.H. St Clair, B.C. Klump, S. Sugasawa, and Z.T. Burns unpublished data). Only non-hooked stick tools have been observed being used during bouts of larva fishing [21,24].

(b) Experimental set-up

Three experimental conditions were presented to wild, free ranging NC crows in October and November 2012. Each condition consisted of two logs, *ca.* 50 cm long, with six holes drilled into each of them at equal intervals (see figure 2). The holes were *ca.* 1.6 cm in diameter and *ca.* 7 cm deep; these dimensions approximately match the median hole depth and width in natural foraging sites [21]. Subjects chose between: a stick vertically inserted into a hole and a stick horizontally resting next to a hole (condition 1); a stick vertically inserted into a hole and a non-inserted vertical stick attached to the end of a log by a thin metal pin embedded into a log and easily removable from the log (condition 2); and a stick vertically inserted into a hole and a stick resting next to a hole presented in conjunction with sawdust (condition 3). Sawdust is an environmental cue signaling the presence of beetle larvae, a hidden prey, that forms a significant proportion of NC crows' diet [21, 26].

In conditions 1 and 3, one log was placed to the left, and the other to the right of a long tree trunk connecting the overhanging branches to the ground, called the 'runway' and always experimenter placed (see figure 2). For condition 2, the logs were placed slightly beyond the base of the runway (maintaining the bidirectional choice) to facilitate the NC crow discriminating between the vertically inserted and the non-inserted stick. The runway provided an unobscured and unbiased way for a NC crow to see both logs prior to interaction with either experimental log. After log placement, the experimental condition was assigned

systematically (to ensure a balanced design) with the vertically inserted stick assigned to one log, and one of three conditions (resting, vertically non-inserted, or resting with saw dust) assigned to the other log. Each twig or leaf petiole was assigned randomly to a log after they were approximately matched for thickness, length, and curvature, as at natural foraging sites. Additionally, matching the tools provided a more realistic choice since the tools left inserted, and the sticks at and immediately around a foraging site have equivalent properties [21].

For all conditions, holes were baited with peanut-sized pieces of meat, and one peanut-sized piece of meat was placed one-quarter and another was placed three-quarters up the runway to encourage interaction with the experimental set-up, and to aid NC crows in overcoming their neophobia. Additionally for condition 2, six peanut-sized pieces of meat were placed at the bottom of the runway to further increase exposure time to the experimental logs, since the logs were moved from slightly under to slightly in front of the runway. All bait were symmetrically placed to ensure an experimentally unbiased NC crow decision.

Trials were defined as a unique interaction by touching the log or any provided stick on the log. Between-trial interchanges and assignments rule out that a certain log, stick, or side of the runway explain the results presented. For each trial, one of three matched sets of logs was used. Logs were interchanged between sites, and new matched pairs of either twigs or leaf petioles were assigned to each trial to avoid pseudo-replication of the stimulus (see [27]). Care was taken to use all holes equally, balance the condition assigned to each log, and to balance the left and right positioning of each log.

Six primary locations were chosen to ensure that previous direct observation of a conspecific interacting with the conditions did not occur since the experiment

had never been performed in the location (and thus statistical independence was achieved), as well as to ensure unmarked birds were unique. The primary choice experiment (condition 1 above) was assigned as the first trial at each unique location, to determine naïve NC crow's inserted stick-tool preference. Subsidiary locations, within each primary location, were used to move the experimental apparatus, enabling encounters with different conditions at unique locations; this ensured that any NC crow participating in multiple conditions encountered each condition at a unique location. All primary locations were baited with meat to increase activity before the experimental conditions were presented.

(c) Data capture and scoring

All encounters were recorded using video (n= 46) or still photographs (n= 5). A majority of videos (n=30) started after the NC crow landed on the runway. Blinds were used to record encounters intermittently for all conditions in some locations. After a trial, the observer waited until all visible birds present during a trial flew out of sight before setting-up the next trial.

Trials were documented in the field using data sheets (ZTB, DS, SS, and BCK). One experimenter (ZTB) scored all video-recorded trials, and subsequently, videos were randomized for a hypothesis-naïve individual to score. The first log (or any stick assigned to the log) touched by the NC crow was scored as the initial choice. Additionally, we scored the following information from all trials: the number of body and head turns the NC crow made before choosing a log, whether or not the scorer believed that the NC crow could have seen both experimental logs at any point prior to making the primary choice, and the behavior of the NC crow on the log (only landing on log, touching a stick on the log, probing with a stick on the

log, or successful extraction of food with a stick; see Table 1 for definitions of each behavior scored). The naïve observer was instructed to use whatever method she wanted to determine whether the NC crow saw both logs.

For the initial log chosen, complete inter-observer agreement occurred between notes recorded in the field on data sheets, the experimenter's scores from re-scoring the videos, and the naïve individual's scores from the videos. Thus, for trials with no video documentation, the score from the field was used for initial log choice only. For all trials with videos, there was 79% agreement between the experimenter and the independent scorer (see 'occurrence agreement percentage' in [28]). All disagreements were reconciled except for the number of body and head turns. Turns were categorized into whether or not they occurred for each trial (summarized below), necessitating both scorers to identify a turn having occurred at least once in the trial. To test whether NC crows turned their head or bodies differently due to condition, the hypothesis-naïve scorer's quantification of head and body turns were used.

(d) Statistical analysis

For all conditions, a trial was designated 'valid' if the NC crow had not previously been on the experimental logs for the specified condition, and could be uniquely identified by either markings (wing tags and/or color rings) or was the first unmarked NC crow at a given location for each experimental condition (see Table 2). One trial was invalidated due to experimenter error, as some bait had not been removed, and was on the ground where the experimental logs were placed.

Binomial choice tests were conducted on initial log choice, and the first hole into which the supplied stick was inserted. A random expectation (P) of 0.5 was

used for both tests. For initial log choice, and after choice validation, this random expectation matched whether the NC crow chose the log with the supplied stick vertically inserted (present in each of the conditions) or the log with one of the other three conditions. For the first hole, the NC crow used the supplied stick to probe; this random expectation tests whether the NC crow chose to probe in the inserted hole or in any other hole. The random expectation of 0.5 ought to be conservative, as there were 6 holes on each log. We additionally conducted a binomial choice test on the first hole into which the supplied stick was inserted with a random expectation of 0.17 (1 out of 6). On three occasions, due to poor video quality, we were not able to determine which hole the NC crow probed. All statistical tests were completed using R [29], and to determine significance, we used an alpha level of 0.05.

Results

Sixteen marked, identifiable individuals participated at four of the six sites alongside unmarked birds at five of the six sites. Across all conditions, 51 successful trials were completed, and among them 31 trials were valid. NC crows exhibited neophobic behavior by: 1) sitting in the trees for a few minutes around the experimental set-up prior to approaching; 2) visiting the runway to eat the pieces of meat several times before making a choice; and/or 3) slowly approaching the logs, and then hesitantly putting either their foot on the log, and/or grabbing the provided stick with their bill. Neophobic behavior did not appear to change throughout the experimental period, though no quantification of neophobic behavior was undertaken.

(a) Validation of choice

To quantify whether or not NC crows saw both presented logs, we counted the number of times a NC crow turned its body and head to face each log. NC crows made at least one body turn and one head turn upon first landing on the runway, in 57% and 78% of all video recorded trials respectively; it was not possible to score head turns in 7 trials because the NC crows did not use the runway. Taking into account all actions prior to making a choice, 96% (44 of 46) of NC crows were scored as having the possibility to see both logs. NC crows did not turn their heads and bodies disproportionately between experimental conditions (head turns: Kruskal-Wallis test, $\chi^2 = 0.64$, df = 2, $p = 0.73$; body turns: Kruskal wallis test, $\chi^2 = 1.65$, df = 2, $p = 0.44$). Additionally, we observed no differences in the amount of time that a NC crow gazed at each stick presentation, suggesting that NC crows did not find a specific stick-presentation to be unnatural, as seen in [30,31].

(b) Initial log choice

To understand NC crow foraging preferences, we quantified the initial log chosen for every trial. NC crows exhibited a highly significant preference for a vertically inserted stick over a horizontally resting stick (see Figure 3, for an example of this choice; condition 1, n = 16, $p = 0.005$). When only using data from the first NC crow at each location to ensure experimental naïvety, the significance of their choice remained unchanged (condition 1, n = 6, $p = 0.03$). Furthermore, all tested NC crows exhibited a significant preference for the inserted stick over a vertical, non-inserted stick, suggesting the ease of picking-up the supplied stick did not drive the preference (condition 2, n = 7, $p = 0.02$). Yet, NC crows lost their significant preference for vertically inserted tools after sawdust, an environmental cue

signaling potential hidden prey, was added to the location of the horizontally resting tool (condition 3, n = 8, $p = 0.7$).

(c) Tool-oriented behaviors on experimental set-up

To determine the potential for tool-oriented information to be indirectly exchanged between crows during a log choice, we quantified tool-oriented behavior on the initial log chosen. NC crows either: 1) left the log without touching the provided stick; 2) picked-up or touched the provided stick; and/or 3) probed with the provided stick. NC crows left the log without touching the provided stick in 11 of 31 trials (condition 1, 5 of 16; condition 2, 2 of 7; condition 3, 4 of 8), touched the stick without probing on the log in 5 of 31 trials (condition 1, 2 of 16; condition 2, 1 of 7; condition 3, 2 of 8), and probed with the stick in 15 of 31 trials (condition 1, 9 of 16; condition 2, 4 of 7; condition 3, 2 of 8). The behavior of subjects at their first-chosen log is summarized, by condition, in Figure 3. In 65% of all valid trials, sticks were touched or used, and in 48% of the valid trials, the tool was used to probe. While in a third of the trials, the tool was not touched, in most of these trials, the NC crow either looked, or probed with its bill, identifying the log as a potential food source.

After choosing to interact with the stick, NC crows made subsequent actions with the stick, such as deciding which orientation to use the stick, and where to probe with the stick. NC crows always used the stick in the orientation provided, never flipping the stick before beginning to probe, suggesting that a conspecific's previous decision with regards to the functional end of the tool and choice of the tool's dimensions, were assimilated into the NC crow's use of the abandoned tool.

In condition 1, NC crows had a statistically non-significant preference, using the most conservative null probability (0.5) to use the inserted stick in the hole in which it was left (n = 8, $p = 0.07$). Combining all conditions, 85% of NC crows probed in the hole into which the stick was initially inserted (n = 13, $p = 0.02$). If the random expectation was adjusted to one-sixth (the choice between holes on a single log), NC crows had a significant preference for deploying the provided stick in the hole in which it was abandoned (condition 1, n = 8, $p < 0.001$; all conditions, n = 13, $p < 0.001$).

Discussion

We show, for the first time, preferential use of abandoned tools in NC crows. NC crows chose a stick inserted into a hole significantly more often than a stick resting on a log. This choice was not driven by the ease of picking up the inserted stick, suggesting that the stick's previous placement, including its insertion, underlies NC crows' preference. Interestingly, NC crows lost their preference for the inserted stick when sawdust, an environmental cue signaling likelihood that a nutritionally valuable beetle larva is present, was added to the location of the resting stick. This loss of preference demonstrates that specific environmental and social factors influence optimal foraging decisions in wild NC crows. Furthermore, after choosing the log with the inserted stick, NC crows preferentially probed in the hole in which the stick was abandoned, suggesting NC crows assimilate social information from the discarded stick's previous deployment, as the stick could only have been inserted by a conspecific [21].

NC crows manipulate stick-like objects from hatching, and, unlike other corvids, develop functional stick-tool use [32]. In the lab, two of four hand-reared

NC crows that were exposed to humans handling stick-like objects, significantly increased their frequency of manipulating sticks compared to the two unexposed NC crows [33]. In the wild, tight knit NC crow family units, consisting of mother, father and offspring, provide the most likely opportunity for direct social influences of tool-oriented behavior as families spend a significantly longer amount of time with each other, than unrelated individuals [20,25,34]. Outside of their family units, juveniles associate with numerous unrelated individuals at close distances, albeit for shorter amounts of time [25]. Herein, we demonstrated an indirect learning process that could be utilized by juvenile NC crows, potentially yielding significant and similar information to that provided by direct observational learning mechanisms. Thus, future work on time-delayed spatial associations could yield comparisons of indirect and direct social learning potentials.

Different types of information are made available, and could be transmitted to a conspecific, when a tool is abandoned, such as the exact foraging location and specific tool properties. An inserted stick enhances certain foraging locations over others, facilitating NC crows to forage preferentially in locations where conspecifics could have previously identified hidden prey [21]. Moreover, NC crows choosing the inserted stick due to its insertion (condition 2) suggests that the evolutionary selection of the choice was driven by the higher potential for hidden prey over other locations. After electing to forage at the location of an inserted stick, NC crows picked-up and probed with the inserted stick in the hole in which it was abandoned. Thus, NC crows are exposed to the exact location where a conspecific used the same tool. Future studies assessing whether or not an inserted stick represents a higher probability of detecting hidden food in the wild will provide evidence towards the evolutionary adaptation of this choice, such as whether an abandoned

inserted tool represents a more successful location to forage than locations with no inserted tools. Through the deployment of the inserted stick, NC crows were shown the properties of tools and, if tool selectivity is established through ontogenetic processes, this exposure could be responsible for the acquisition of tool selectivity of certain physical properties (*e.g.* length, diameter [35,36]; as discussed in [21,23]). At first use, NC crows did not alter the end of the tool being inserted into the log. Thus, NC crows encountered a conspecific's decision regarding which end of the tool was inserted to probe for beetle larvae. There is insufficient understanding of the quantity and quality of information NC crows can gather from abandoned tools, and future work is needed to determine what properties of abandoned tools NC crows can acquire without direct observation of conspecifics.

Information from abandoned objects could be a significant factor in the spread and maintenance of tool-use in wild populations. We hypothesize that the use of abandoned tools may facilitate juvenile tool-users to acquire an efficient tool-oriented deployment strategy, similar to 70% of juveniles utilizing the most efficient stripping strategy without direct observation after being exposed to semi-stripped pinecones [3]. Additionally, abandoned objects could be the only stimulus required to solve a foraging task, if and only if, necessary cognitive predispositions are present. For example, non-natural tool-users, Japanese macaques (*Macaca fuscata*), were able to solve a tube task after only being exposed to inserted tools left in the apparatus [37,38], yet savannah baboons (*Papio anubis*) were unable to solve a similar task during an experimental period [39]. Future work is needed to assess the role of abandoned objects facilitating the acquisition of novel foraging behaviors, potentially revealing necessary social, environmental, cognitive, and genetic factors.

The rigor of collecting data from wild animals yields unique experimental design challenges and limitations. In our study, the vertical stick attached to the end of the log could be perceived as unnatural by the NC crows. Nonetheless, the number of head turns was not significantly different between conditions, and no evidence of a NC crow fixating on the vertically attached stick was observed, as might be predicted if the condition was perceived as unnatural [30,31]. Additionally, different types of twigs and leaf petioles were attached to the log, reducing the possibility that NC crows might have seen the stick as part of the log. The overall design of the experiment was non-randomized through time. Condition 1 was performed first in every location (to ensure enough naïve subjects for condition 1), with condition 2 and 3 being implemented thereafter. Thus, another possible confounding factor on condition 2 and 3 is that subjects might have observed other NC crows making a particular choice, or personally experienced success with the inserted stick. We addressed this by randomizing the left and right placement of the inserted stick, and by ensuring that NC crows did not have previous experience at that specific testing location, as all NC crows being tested were at a different specific (but same principal) locations. Furthermore, if NC crows learned to associate the inserted tool with food, the outcome for condition 3 (with more crows choosing the resting stick with saw dust than the inserted stick) is non-parsimonious. Therefore, the most likely explanation for NC crow choice excludes utilizing previous direct observations of conspecific's choices to influence the NC crow's log choice.

We demonstrated that NC crows have a preference for abandoned inserted tools, revealing an indirect process whereby social information can facilitate the acquisition of tool-oriented behavior. Future work focusing on the role of

abandoned tools amongst juveniles will be important to demonstrate motor actions that necessitate direct observation of others, and subsequently, to elucidate the role of trial-and-error learning, indirect social learning, and direct social learning in tool-oriented behavior. Additionally, experimentally manipulating different information that can be obtained from the abandoned tool, such as tool properties, will demonstrate the value of indirect processes in the selection of tool characteristics. The role of indirect social influences is essential to understand the maintenance and spread of tool-oriented behaviors.

Ethical Review

The University of Oxford's local ethical review committee approved experiments for the duration of the research grant (BBSRC) that funded this work; recently, this grant has been transferred from the University of Oxford to the University of St. Andrews.

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Figure 1. **(a)** New Caledonia is situated in the South Pacific, approximately 1200 km off the east coast of Australia. **(b)** All experimental sites were midway along the west coast of New Caledonia. **(c)** Primary locations (marked with numbered, red pins) where the experiments were performed at: *Site 1*- Dry forest site 1, *Site 2*- Dry forest site 2, *Site 3*- Farmland site 1, *Site 4*- Dry forest site 3, *Site 5*- Farmland site 2, *Site 6*- Human disturbed beach site. All sites are greater than one kilometer apart with the closest being sites 1 and 2 at *ca.* 1200 m. Maps for panels (a), (b), and (c) are from Google, with data supplied to Google by SIO, NOAA, U.S. Navy, NGA, and GEBCO; all maps are used in accordance with fair use guidelines.

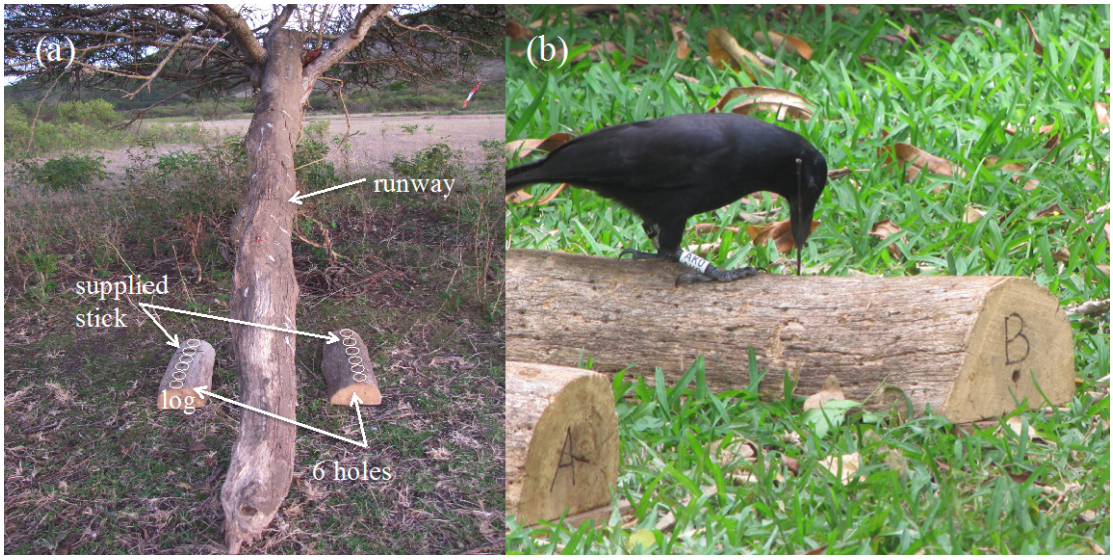

Figure 2. (a) The experimental set-up consisted of two logs, each with six holes. One log was placed to the left, and the other to the right of the runway, a log connecting the overhanging branches to the ground. A stick was inserted into an assigned hole of one log and the equivalent hole of the other log was assigned one of three conditions (resting stick, vertically attached stick, or a resting stick in conjunction with an environmental cue, sawdust). Each hole contained a single peanut-sized piece of meat, and two peanut-sized pieces of meat were placed on the runway. For the vertically attached stick, the logs were moved to the base of the runway, maintaining the bidirectional choice, and six additional pieces of meat were symmetrically placed on the runway. **(b)** A New Caledonian crow probed with a supplied leaf petiole on the experimental set-up.

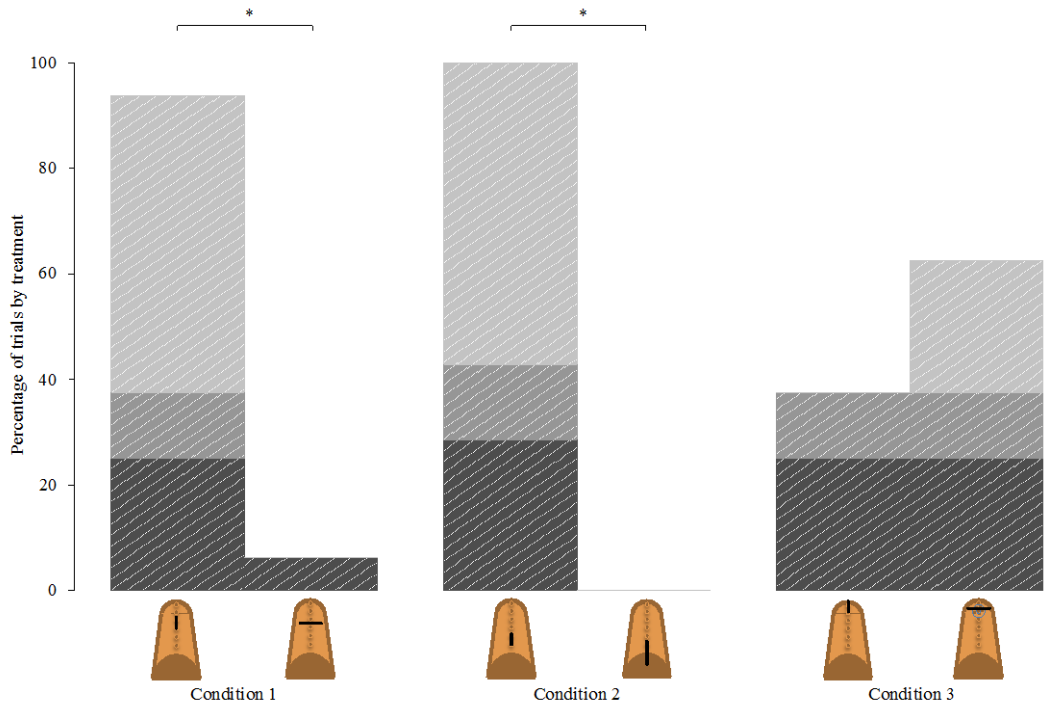

Figure 3. Percentage of time New Caledonian (NC) crows chose one log in each condition alongside foraging behaviors, shown as 'no contact with stick' (dark grey), 'touches stick' (grey), and 'probes with stick' (light grey). Condition 1 is a choice between a stick vertically inserted into a hole, and a stick resting next to a hole; condition 2 is a choice between a stick vertically inserted into a hole and a vertically non-inserted stick attached to the end of a log by a hidden pin; and condition 3 is a choice between a stick vertically inserted into a hole, and a stick resting next to a hole in conjunction with sawdust, a known environmental cue signaling hidden prey. NC crows preferred the inserted tool in conditions 1 and 2 (condition 1, Binomial choice test, random expectation (P) = 0.5, n = 16, $p = 0.01$; condition 2, Binomial choice test, random expectation (P) = 0.5, n = 7, $p = 0.02$), and no longer preferred the inserted tool in condition 3 (Binomial choice test, random expectation (P) = 0.5, n = 8, p = 0.7).

Table 1. Definitions of scored New Caledonian (NC) crow behavior.

Measured behavior	**Definition**
Body turn	Between the first touch of the runway and initial choice (see below), the number of times the mid-section of the crow's body changed between facing the log on the left to facing the log on the right, and vice-versa.
Head turn	Between the first touch of the runway and initial choice (see below), the number of times the crow's head changed between facing the log on the left to facing the log on the right, and vice-versa.
Potential to see both logs	Whether or not the NC crow, from the time the video started until a choice was made, had the potential to see both logs.
Initial choice	The first log, or any stick inserted, attached or resting on the log, touched by the NC crow
Tool-oriented behavior	***No contact with stick*****:** The NC crow touched either the log or supplied stick with part of its body, but did *not* touch the supplied stick with its bill. ***Touches stick*****:** The NC crow touched the supplied stick with its bill. ***Probes with stick*****:** The NC crow inserted the supplied stick with its bill into a hole in the log and/or repeatedly moved it up and down in a controlled manner.

Table 2. Experimental timeline. Lines marked in **bold** are valid trials: a trial was valid if the New Caledonian (NC) crow had not been on the experimental logs for the specified condition and could be uniquely identified, or was the first unmarked NC crow at a given location for that experimental condition. **Date**: date of trial. **Time**: time NC crow landed on log. **Trial**: ordered trial number by date and time. **Location**: one of six principal sites where conditions were placed (see figure 1c): *Site 1*- Dry forest site 1, *Site 2*- Dry forest site 2, *Site 3*- Farmland site 1, *Site 4*- Dry forest site 3, *Site 5*- Farmland site 2, *Site 6*- Human disturbed beach site. **Condition**: conditions presented to the NC crows included, 1- stick vertically inserted into a hole versus a stick resting next to a hole, 2- stick vertically inserted into a hole versus a vertically attached non-inserted stick, 3- stick vertically inserted into a hole versus a stick resting next to a hole in conjunction with sawdust (an environmental cue of hidden prey). **Subject**: a unique wing-tag or plastic ID rings combination to determine individuals. Wing-tag colors appear as left wing tag color, right wing tag color, and then a number (if visible): B: blue, G: green, Y: yellow, O: orange, P: pink, W: white, R: red. ID rings contain two letters followed by a number. **Conspecifics present**: description of other individuals visible to the experimenter. 'WT' – wing tag, question marks (?) identify unknown pieces of a unique identity. 'UNK'- one other individual seen but no unique identifiers were visible.

Date	Time	Trial	Location	Condition	Subject	Conspecifics present
16-Oct-12	10:04	1	5	1	UNMARKED	-
17-Oct-12	13:55	2	5	1	UNMARKED	-
17-Oct-12	16:35	3	5	1	UNMARKED	AR9
22-Oct-12	**9:26**	**4**	**1**	**1**	**HC0**	**Other WT NC crow (colors unknown)**
23-Oct-12	**9:23**	**5**	**1**	**1**	**P-B**	**-**
23-Oct-12	**11:00**	**6**	**1**	**1**	**O-O**	**Other WT NC crow (colors unknown)**
25-Oct-12	**8:36**	**7**	**1**	**1**	**Y-Y**	**B-G; Y-?**
25-Oct-12	**9:35**	**8**	**1**	**1**	**R-O**	**-**
25-Oct-12	**9:38**	**9**	**5**	**1**	**O-P (1)**	**B-O; P-W**
25-Oct-12	11:49	10	1	1	R-O	UNK at vocal distance
26-Oct-12	7:31	11	1	1	R-O	G-O; ?-Y
26-Oct-12	8:15	12	1	1	R-O	-
26-Oct-12	**9:56**	**13**	**1**	**1**	**UNMARKED**	**B-B**
27-Oct-12	**7:45**	**14**	**2**	**1**	**P-W**	**P-Y on log displacing P-W**
27-Oct-12	9:16	15	2	1	P-W	-
27-Oct-12	10:17	16	2	1	P-W	-
27-Oct-12	10:20	17	1	1	R-O	-
27-Oct-12	**11:03**	**18**	**2**	**1**	**UNMARKED**	**1 unmarked**
28-Oct-12	**6:43**	**19**	**2**	**1**	**P-Y**	
28-Oct-12	7:15	20	1	1	R-O	1 unmarked at distance
28-Oct-12	8:24	21	1	1	R-O	Y-O on log
28-Oct-12	10:34	22	1	1	Y-O	-
28-Oct-12	**17:29**	**23**	**5**	**1**	**B-O-13**	**1 unmarked on log, 1 other WT crow (colors unknown)**
3-Nov-12	5:50	24	1	1	R-O	Many NC crows at vocal distance
3-Nov-12	9:05	25	1	1	UNMARKED	Y-Y
3-Nov-12	**10:50**	**26**	**1**	**1**	**O-P (2)**	**R-O; 1 other UNK**
4-Nov-12	**10:20**	**27**	**1**	**3**	**R-O**	**-**
6-Nov-12	10:25	28	6	1	CU2	-
8-Nov-12	**9:15**	**29**	**6**	**1**	**AK0**	**CU2**
8-Nov-12	**11:10**	**30**	**6**	**1**	**CU2**	**AK0 on log; ES8**
10-Nov-12	5:42	31	1	3	R-O	-
11-Nov-12	**6:55**	**32**	**1**	**3**	**HC0**	**O-Y; 1 unmarked**
11-Nov-12	**8:50**	**33**	**2**	**3**	**P-Y**	**W-W**
11-Nov-12	**10:20**	**34**	**2**	**3**	**UNMARKED**	**-**
13-Nov-12	8:00	35	2	3	UNMARKED	-
13-Nov-12	**11:40**	**36**	**1**	**2**	**R-O**	**8 others in sight**
14-Nov-12	**9:46**	**37**	**1**	**2**	**UNMARKED**	**2 other unmarked on other log**
14-Nov-12	**9:46**	**38**	**1**	**3**	**UNMARKED**	**1 unmarked; 1 unmarked on other log**
14-Nov-12	**11:39**	**39**	**1**	**2**	**HC0**	**1 unmarked displaced from runway**
15-Nov-12	**6:46**	**40**	**1**	**2**	**B-B**	**1 unmarked**

Date	Time	Trial	Location	Condition	Subject	Conspecifics present
15-Nov-12	**7:49**	**41**	**1**	**2**	**Y-Y**	**P-P; 1 unmarked**
15-Nov-12	**11:04**	**42**	**1**	**2**	**G-Y**	**B-W; 1 other WT (colors unknown)**
15-Nov-12	11:31	43	1	3	UNMARKED	-
16-Nov-12	**9:00**	**44**	**1**	**3**	**R-R**	**1 unmarked**
17-Nov-12	**6:25**	**45**	**3**	**1**	**UNMARKED**	**2 other unmarked**
17-Nov-12	**9:52**	**46**	**4**	**1**	**UNMARKED**	**-**
18-Nov-12	**12:06**	**47**	**2**	**2**	**P-Y**	**O-W displaced from runway**
19-Nov-12	**8:01**	**48**	**1**	**3**	**Y-Y**	**?-B**
20-Nov-12	6:47	49	2	3	P-Y	O-W
20-Nov-12	8:15	50	1	3	R-R	R-O; Y-B
21-Nov-12	**6:20**	**51**	**4**	**3**	**UNMARKED**	**1 unmarked**

CHAPTER 8

SOCIAL ORGANIZATION OF WILD NEW CALEDONIAN CROWS IS CORRELATED WITH SPACE USE: QUANTIFYING THE POTENTIAL FOR INDIRECT INFORMATION EXCHANGE VIA TOOL ARTEFACTS

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Social organization of wild New Caledonian crows is correlated with space use: Quantifying the potential for direct and indirect information exchange

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Abstract

Association patterns are non-random in nature, determined by both animal- and environment-based factors. With the development of high-resolution methods to collect animal-to-animal associations concurrently with an animal's use of the environment, research has begun to quantify factors responsible for social network topology. While some studies have investigated the role of space-use with direct information exchange, no study has connected the use of space with the ability to learn from artefacts of other animals. Here, we investigate the role of space use on direct and indirect information exchange in 33 wild New Caledonian (NC) crows. First, we calculated each NC crow's home range, revealing an average space use after 7 days of 0.33 km^2 using minimum convex polygons, and 0.11 km^2 using a 95% fixed kernel density estimator. Then, we quantified the home range overlap for each pair of NC crows, revealing significant overlap between individuals living within the same community. Next, we compared this dataset with their known social associations, revealing that shared space use is highly correlated with the observed social structure, even after controlling for the underlying genetic structure. Furthermore, relatedness is not correlated with home range overlap, suggesting that shared space use and genetics are independent drivers of NC crow network topology. Altogether, these findings suggest that NC crows' shared space use is a significant factor in determining both direct and indirect encounters with other NC crows or their artefacts, respectively. Moreover, shared space use could be a significant factor in the rate of cultural information exchange between wild NC crows.

Introduction

Animals interact with each other, and monitoring these associations is the *modus operandi* of scientists seeking to understand their sociality (Krause and Ruxton 2002). Over time, quantifying who associates with whom produces the social structure of the study population, typically revealing animals interacting more or less often with others (Hinde 1976). Correlating different factors with association patterns could expose underlying processes to test, such as relatedness or space-use, that drive animals' decisions regarding with whom and for how long to associate. Thus, measuring the social organization and determining the underlying factors driving social structure are essential to predict the likely processes by which socially mediated behaviors are acquired.

Age, sex, kinship, and/or use of the environment have been shown to drive social structure in numerous faunae. For example, an animals' use of the environment, quantified through home range overlap, partially governs Reticulated Giraffe (*Giraffa camelopardalis*) association patterns (Carter *et al*. 2013, Vanderwaal *et al*. 2014), and kinship drives fission-fusion dynamics in wild Elephants (*Loxodonta africana*), potentially persisting for decades after the death of the original maternal kin (Archie *et al*. 2006). Moreover, controlling for age, sex, and space-use can reveal additional factors driving social structure. In bottlenose dolphin communities, the ability to perform a task, namely the use of sponges to protect their beak during foraging, is correlated with association patterns (Mann *et al*. 2012), specifically demonstrating that social partners are determined, in part, by whether or not an individual uses tools.

While the methods to determine which factors that drive social structure have advanced considerably, wild birds have for the most part eluded quantification

due to the difficulty of recording reliable associations (except, *c.f.* Aplin *et al*. 2012, Rutz *et al*. 2012). To bridge this gap, biotechnologies have been developed and refined to collect autonomously high-resolution data to measure associations between individuals (Rutz and Hays 2009, Krause *et al*. 2013). An easy-to-access wild population of blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), and marsh tits (*Poecile palustris*) was fitted with RFID tags, or passive transponders, which recorded associations at specific locations containing receivers, revealing a strong correlation between patch discovery and sociality; this finding suggests that the more social an individual is at a foraging site the more likely that individual is to discover a novel patch of food (Aplin *et al*. 2012). A study on another wild species, New Caledonian crows (*Corvus moneduloides*; hereafter NC crows) revealed that kinship was a factor in determining social structure (Chapter 5, 6, Rutz *et al*. 2012). Furthermore, during an experimental manipulation, the correlation between associations and relatedness was removed, and after the removal of the experiment, the correlation was restored (Chapter 4, 5). Therefore, the genetic barrier to direct information transfer was removed as a consequence of a community-centric experimentally placed food glut (Chapter 5). In addition, while a previous study investigated home range size of wild NC crows on Maré Island, revealing an average space use of *ca.* 0.8 km^2 for 6 females, this study did not discuss the overlap of home ranges or suggest that home ranges dictate any form of sociality (Holzhaider *et al*. 2011).

While previous work with wild NC crows investigated direct information exchange abilities, no study has yet investigated the potential for indirect information exchange. Wild NC crows live in an environment with considerable variation in the length and diameter of sticks, and foraging NC crows alter the

distribution of sticks at prospective foraging locations (Bluff *et al*. 2010). In addition, wild NC crows have been shown to select inserted sticks, rather than horizontally resting or vertically presented sticks (see chapter 6). The unique distribution of stick-tools at these foraging sites and the selective preference of NC crows for inserted stick-tools suggest that tool-related properties can be exchanged without direct observation of a conspecific. Thus, understanding the probability of re-using a conspecific's tool is essential to further understand the pathways for information exchange in wild NC crows.

In this study, we aimed to investigate whether space-use correlates with associations and if NC crows have overlapping space use with multiple NC crows. Methodologically, we quantified the home range for each NC crow and measured the overlapping space, home range overlap (HRO), between each pair of NC crows. To define the number of associations possible due to HRO, we quantified at every percentage overlap the number of crows in association. To determine whether space-use correlates with associations, we correlated a matrix of HRO with associations. Next, to elucidate whether a correlation between space-use and associations was independent of first-order relatedness and community structure (as presented in chapter 4 and chapter 5), we controlled for first-order relatedness and community identity.

Methods

Data collection

Encounternet is a proximity logging system (Krause *et al*. 2013) consisting of three components—tags, basestations, and a yaggi antenna (for a description of *Encounternet*, see (Rutz *et al*. 2012, Chapter 2, 4, 5). Tags were attached to NC

crows, after being programmed to transmit ID-, date-, and time-encoded radio-signals every 20 seconds. Tags aggregated received pulses into 5-minute encounters, recording a maximum, minimum, and mean received power. Tags were programmed to pulse from 4:00 to 20:00, which included all daylight hours as well as the beginning and end of roosting.

Basestations were deployed in our long-term study site (Bluff *et al*. 2010, Rutz *et al*. 2012), consisting of two interconnected valleys, with a hill separating the valleys in the north, and a forested area at the intersection of the two valleys in the south. Basestations that were deployed within the environment formed a Wireless Sensory Network, recorded all pulses sent by the tags, and downloaded all association logs recorded by each tag. Since basestations only performed a single task at a given time, basestations were programed with a priority to download logs, and secondarily to record pulses. While the principal function of each basestation was to download data, the amount of time to download logs should not adversely affect the basestation's ability to record pulses. To ensure basestations were not constantly downloading logs, we programmed basestations to only record logs after a threshold was met: logs were downloaded if 64 encounters were detected in central basestations, and 18 encounters occurred in peripheral basestations. To ensure basestations and tags were operating as programmed, we communicated with all components using a yaggi antenna. In addition, we downloaded all logs from basestations (and tags as necessary) using the yaggi antenna.

Home-range size

There is an on-going debate about the best method to measure home ranges, such as the use of minimum convex polygons (MCP) and functions (*e.g.* kernel-density, or

KDE) that estimate home ranges based on probability densities (Seaman et al. 1999; Calenge 2006; Horne and Garton 2006; Row and Blouin-Demers 2006; Frère *et al*. 2010). MCP methods generate a home range for each animal by connecting the outermost points recorded for an animal, yet lack any ability to describe the time an animal spends in each location. In comparison, kernel-density, and similarly derived, functions utilize the differences in recording frequency at each location to estimate a home range that includes the most-likely location for each animal. Importantly, neither method suggests whether or not an animal uses that specific part of its home range (Horne and Garton 2006). Thus, I calculated home range sizes using both MCP and KDE, following the methods of numerous previous studies (*c.f.*, Horne and Garton 2006).

Home range size was calculated using the 'adeHabitatHR' package in R (R Development Core Team). MCP-derived home ranges used 100% of the points, as we sought to understand the maximum space each NC crow used. A KDE using a 95% probability contour was used to quantify a core home range for each NC crow, paralleling the methods of numerous studies (Seaman et al. 1999; Calenge 2006; Horne and Garton 2006; Row and Blouin-Demers 2006; Frère *et al*. 2010).

We constructed social networks of wild NC crows over four different time periods: 1) a 7-day undisturbed period, 2) a 3-day food-glut occurring in a spatially centralized location, 3) a 4-day manipulation with the removal of the first food-glut, and the placement of two spatially separated food gluts, and 4) a 5-day undisturbed period upon removal of the 4-day experimental food glut (for a full description see Chapter 5). To isolate associations corresponding to periods of social activity, association networks were limited to associations that occurred post-sunrise and pre-sunset (*i.e.*, removing the roosting period from the dataset).

To compare the home ranges between the baseline and experiment 2 time periods, a random sample of four days was selected from the baseline (and all other day combinations checked) to compare against the four days of experiment 2. To test for differences in home-range size, a paired sample Wilcoxon signed rank test (with pairing based on bird ID) was performed in R.

Network construction

The overlap of 'home-ranges' for each specified time period provided the core data for the space-use matrix. For a similar network in Reticulated Giraffes, see Vanderwaal *et al*. (2014). Once home ranges were established, overlap in home ranges was determined using the space that crows co-occupied divided by the combined size of both crow home ranges; these values were placed into the spatial association matrix. We used the package 'adeHabitatHR' within the R platform to conduct analyses.

Two comparisons were to be made with the home range overlap network: direct associations measured from tag-to-tag exchanges, and a genetic network. A binary matrix of first-order relatedness (related is 1, non-related is 0) was created, and was previously presented in Chapter 5. First-order genetic relatedness and bird sex were determined through molecular techniques, as explained in (Rutz *et al*. 2012). Age was determined through the coloration of the gape, as explained in (Rutz *et al*. 2012, Chapter 5). Communities were also determined in a previous study, and we will use those designations herein (see Chapter 5). Social families were determined through consistent daily associations consisting of at maximum an adult male, an adult female, and a juvenile; some social families consisted of a single adult and juvenile (we most likely did not trap the other social adult): see,

Holzhaider *et al*. 2010, Holzhaider *et al*. 2011, and Hunt *et al*. 2012 for additional information regarding the social structure and family life of wild NC crows.

Statistical analyses

Home ranges were quantified using MCP and KDE methods described above with home range size calculated in km^2. To quantify the home range overlap (HRO) and, thus, the probability of indirect information exchange, we calculated the percent overlap with each crow using KDE measures, since KDE was more conservative on time spent in each location. We assume that the probability of foraging is equal, and the time of day that two birds associate is random during each day. The overlapped space will be different, as we calculate overlap by taking the shared space over the total space for a NC crow. For example, if NC crow 'A' had a home range of $0.6km^2$ and NC crow 'B' had a home range of $0.3m^2$, and they shared $0.03m^2$, the HRO for crow 'A' would be 5% and for crow 'B' would be 10%. To analyze the effect of shared space use and genetics on direct associations, we used a Mantel test constrained by community identity (see Chapter 4). Finally, we used a Mantel test to determine the daily correlation between genetics and space use, with or without constraints for community identity. We used an alpha value of 0.05 for all statistical tests, unless otherwise stated.

Results

Home range size was calculated for 33 free-ranging NC crows (Figure 1); home ranges were calculated cumulatively through time (*e.g.*, day 2 consists of a home range that includes space-use from day 1 and 2; day 3 includes days 1, 2, and 3, etc.). After seven undisturbed days using MCP, the mean home range size was 0.33

km^2, and the median home range size was 0.30 km^2 (range: 0.04 to 0.76 km^2); after 19 days, the mean home range size was 0.41 km^2, and the median home range size was 0.36 km^2 (range: 0.04 to 0.89 km^2). After seven undisturbed days using KDE at 95%, the mean home range size was 0.11 km^2, and the median home range size was 0.08 km^2 (range: 0.0016 to 0.37 km^2); after 19 days, the mean home range size was 0.089 km^2, and the median home range size was 0.067 km^2 (Figure 2; range: 0.0025 to 0.36 km^2). MCP estimates were expected to be larger than KDE estimates, as MCP estimates require a single observation to include a location in the polygon. Interestingly, home ranges built from MCP methods did not contract due to experimental conditions (baseline: days 299 – 302; experiment 2: days 309 – 312; paired Wilcoxon sign rank test; $p = 0.23$—all combinations of days from baseline are non-significant).

To quantify the HRO between each pair of NC crows, we used KDE estimates (Figure 3). KDE estimates are better for two reasons: 1) home range size was always smaller than MCP methods, allowing less space to be shared and the shared space to include the locations used most often, and 2) the probability that two crows shared a space would exclude sallies. To explore whether HRO is a driver of NC crow associations, we quantified the correlation between HRO and association data. HRO is significantly correlated with associations each day (Figure 4; community constrained mantel test; $p < 0.002$ for all days). There was no difference in correlation between HRO and association patterns based on experimental condition after correcting the alpha level for multiple test comparisons using a Bonferoni correction (Kruskal-Wallis test; $\alpha = 0.0125$; $X^2 = 8.06$; $p = 0.045$). The correlation between space use and associations is maintained even after controlling for relatedness (constrained partial mantel test; $p < 0.002$ for all days),

suggesting that space-use is an independent factor from first-order relatedness in determining sociality. In addition, we revealed no correlation between first-order genetic relatedness and home-range overlap (mantel test, $p > 0.05$ for all days).

To calculate the probability for indirect information exchange, we used the overlap calculated by KDE estimates, as described above. Due to methodology, we were unable to differentiate the visitation of locations *after* an individual, and these associations may have occurred at the same time. Juveniles have a minimum HRO of 95% with their social family (Figure 5), and we observed a trend for juveniles to have a larger HRO in relation to related adults compared to HROs with unrelated adults (Wilcoxon test; $n = 3$; $p = 0.063$). In addition, we revealed that NC crows share their home ranges with *ca.* 70% and 45% of conspecifics in the Northern and Southern communities, respectively (Figure 6).

Discussion

The mean home range size of wild NC crows match the male-only home range sizes presented for males in Holzhaider *et al*. (2011); we found no differences in home range due to age or sex (Figure 1). Interestingly, we did not measure any contraction of home range size during our experimental time period, suggesting that a localized food source was not sufficient to prevent movement across their home ranges as measured in the undisturbed period. We revealed that HRO is correlated with associations between NC crows even after controlling for relatedness and community structure (Figure 4). Moreover, we demonstrated that there is no correlation between genetics and space use, suggesting that both contribute independently to the variation attributed to associations. In addition, we revealed

HROs within communities (Figure 3 and 6), suggesting that a single individual could discover tools abandoned by numerous NC crows.

Space use is correlated with associations, even after controlling for the variation attributed to first-order relatedness and community membership; moreover, HRO and genetics are not correlated, suggesting at least two independent factors determine associations. Together, our results suggest that space-use is a significant factor determining who could acquire information from whom: a central question surrounding the suspected cultural transmission of information in wild crow populations (Hunt and Gray 2003). NC crows use multiple tool types and manufacture multiple tool designs, each of which is passed onto the next generation potentially through a mix of genetic, ecological, and social components (for a review, see Rutz and St Clair 2012). While we do not understand which, if any, components of NC crow tool-use or manufacture rely on social information, understanding from whom each NC crow could learn suggests the most heuristic explanation to include close family for sustained encounters, numerous brief encounters, and numerous individuals contributing to the use of abandoned tools (Chapter 6).

Previous studies have observed juvenile NC crows closely following their parents (Holzhaider *et al*. 2010; Hunt *et al*. 2012). We demonstrated that juveniles share a minimum of 95% of their home range with their social family (Figure 5); yet, they share more than half of their home range with multiple other NC crows. While direct information exchange is likely from adult social family members to juveniles, tools abandoned within the environment are likely to be another NC crow's tools. Moreover, we demonstrated that, if the probability of tools being left inserted is the same for all NC crows, an abandoned tool in a given location could

come from many NC crows, as there are numerous NC crows overlapping in the same location. Since adult NC crows prefer inserted tools at foraging sites (Chapter 6) and these tools are likely to be the tools of another individual, juvenile NC crows are exposed through their social parents to the tools of other NC crows. Therefore, juveniles are likely to encounter tool-properties from conspecifics, which could reinforce a population level selection of specific tool lengths or diameters (*c.f.* Chappell and Kacelnik 2002, 2004, Bluff *et al*. 2010).

We used the quantification of HRO to discuss the potential for indirect information to be exchanged, a notion that to the best of our knowledge is not yet utilized in the literature. This focus will allow for a more refined mapping of the exchange of information between NC crows, and is useful for other animals that acquire information from artefacts, such as scent marking (Ralls 1971) or scratching bark off trees to mark territorial boundaries (Feldman 1994). Similarly, other species use tools and leave them behind in foraging locations. For example, wild chimpanzees and capuchin monkeys (Fragazsy *et al*. 2013) could acquire information from artefacts facilitating cultural differences, as repeating patterns of use without direct observation would be more erroneous than those with direct observation (*c.f.* Terkel 1996, Aisner and Terkel 1992). Therefore, mapping the overlap of a shared environment yields a framework to explore from which individuals an animal can acquire information.

While conservative statistical tests were used, the method used here has a few limitations. First, the deployed base stations were 1) optimized between collecting spatial data and collecting association data from crow tags; and 2) were deployed along the length of a river bed, with only three base stations placed on the side of the ridge. Because a perfect grid of base stations was not deployed, we might

have underestimated the home ranges of NC crows due to edge effects. However, the home range size estimated herein matches the home range size of another study (Holzhaider *et al*. 2011), and qualitative observations of NC crows traveling more consistently up and down the riverbed (valley), rather than traveling over hills to adjacent valleys.

Interestingly, we quantified for the first time the use of space to estimate the potential of indirectly finding another individual's abandoned tools. With HROs between multiple birds at a single location, a recovered abandoned tool could have originated from any of these birds. In addition, while juvenile NC crows share equivalent home ranges of their social family, the abandoned tools used by their parents remain the tools selected by non-social family NC crows. Thus, tool properties are likely horizontally and/or obliquely transmitted between non-related and/or non-family crows to juveniles acquiring tool-oriented behaviors.

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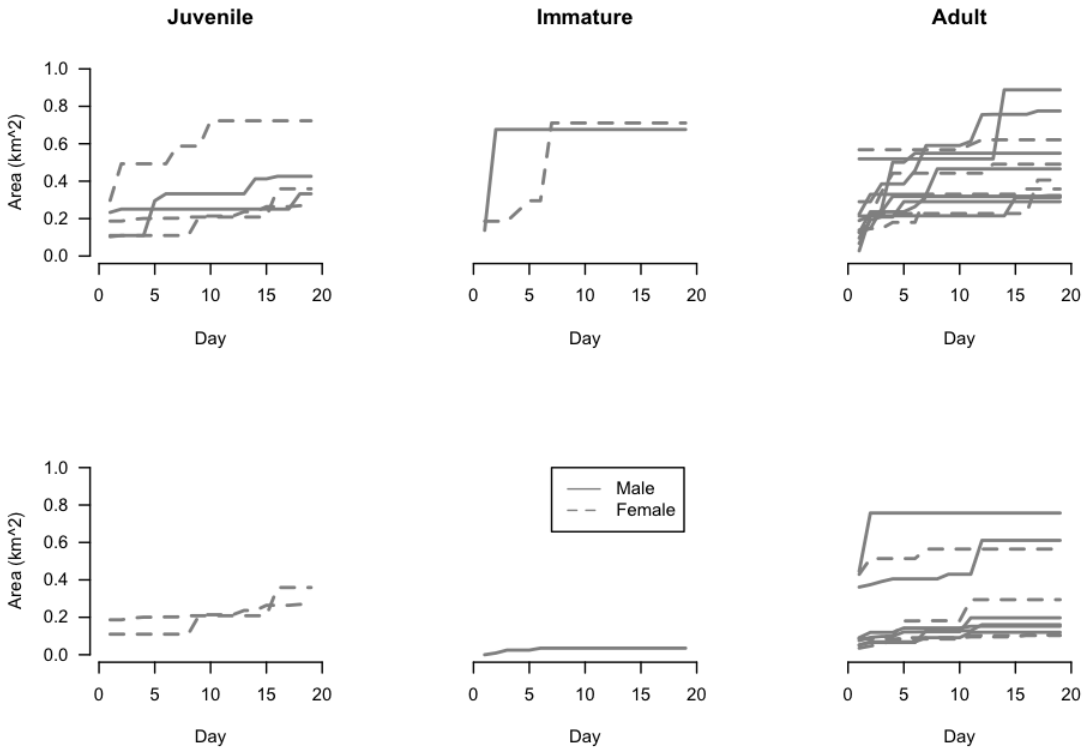

Figure 1. Home range sizes for 32 wild New Caledonian crows. Home range sizes per bird were cumulatively calculated each day (*e.g.*, day 2 consists of a home range that includes space-use from day 1 and day 2; day 3 includes days 1, 2, and 3; etc.). Home ranges on the top row are from the Northern community, and home ranges plotted on the second row are from the Southern community. Home ranges are sub-divided in columns by age class with solid (male) or dashed (female) lines within each plot signifying sex.

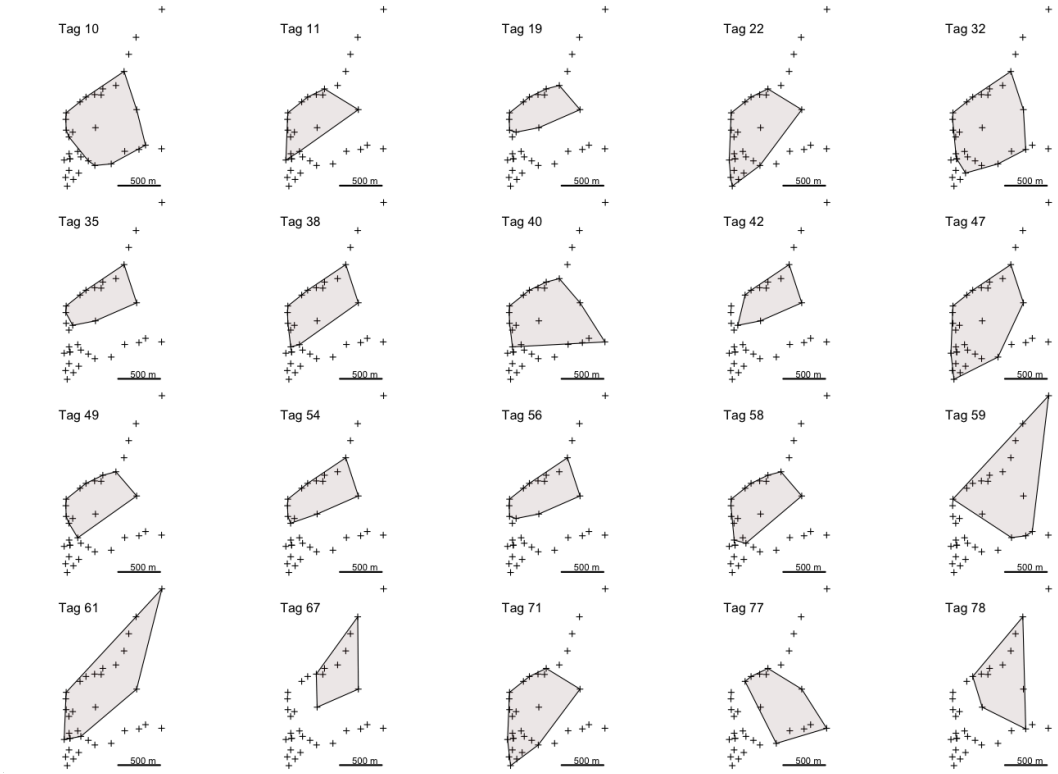

Figure 2. Home ranges for Northern community NC crows using a minimum convex polygon for all 17 days. Each + symbol is a base station, and the home range is depicted by a grey-shaded polygon. Tag ID is labeled next to its home range, and each solid line on the bottom right of each home range is 500 meters.

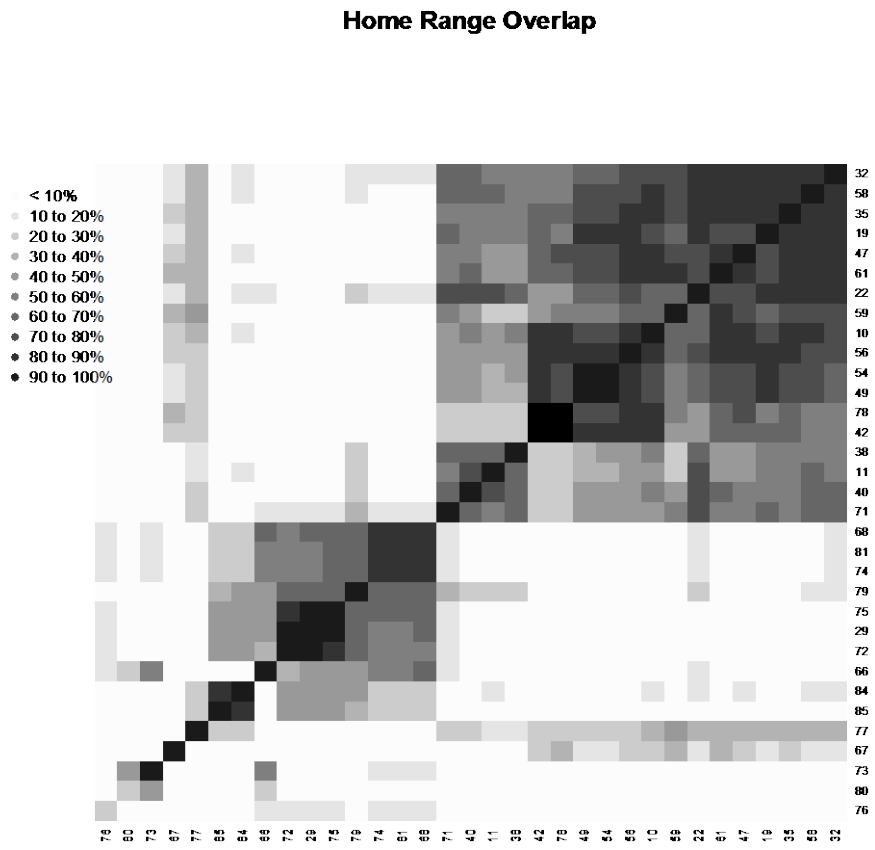

Figure 3. Home range overlap (HRO) of 33 wild New Caledonian (NC) crows for 17 days. Home ranges were built for each NC crow using a fixed kernel density estimator with a 95% probability contour. The union of each pair of NC crows' home ranges was determined, and the shared space as a proportion of the size of their home range defined the HRO. The HRO is different for each pair of NC crows, as each bird will have a unique home range size, and thus the overlap with another NC crow will be a different percent of its home range. There are two communities visualized by the two darker larger squares (*topright* is the Northern community and *bottomleft* is the Southern community), revealing a larger HRO within communities than between communities. Darker colors represent more home range overlap. Bird IDs are given on the axes. Bird IDs are ordered in a dendrogram weighted scheme, which maximizes blocks of associations.

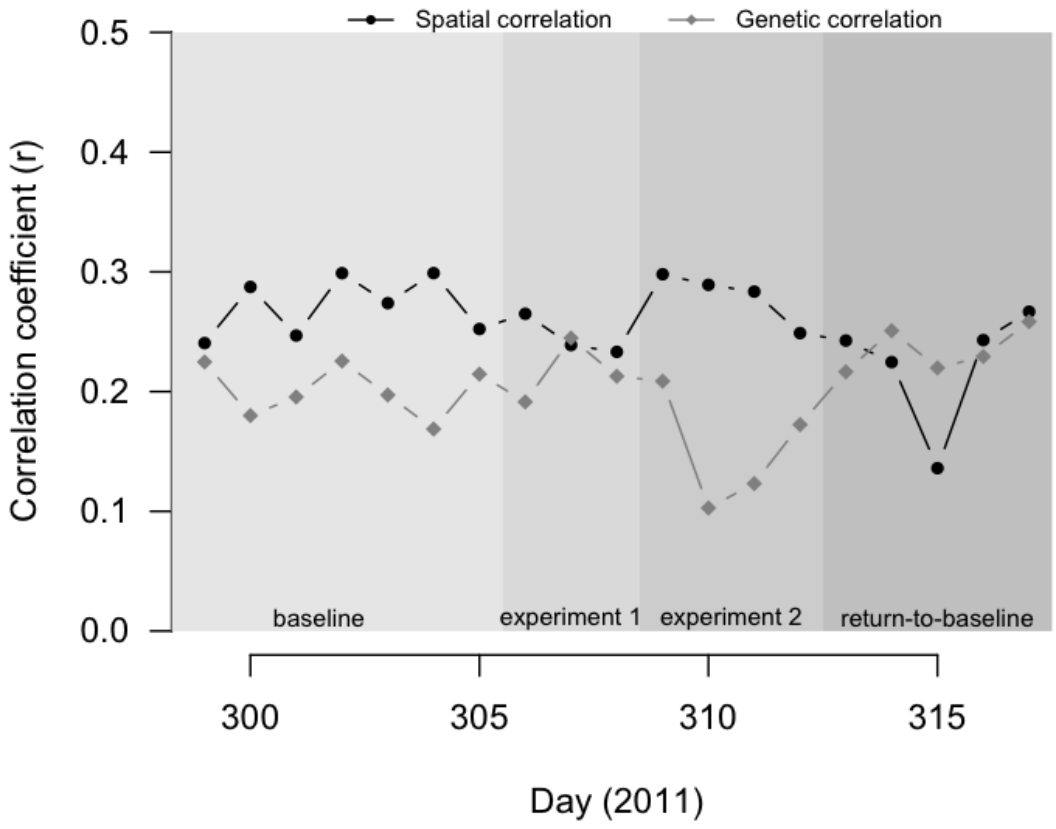

Figure 4. The correlation of associations with space-use and relatedness across four experimental treatments. Each day, a significant correlation between a NC crow's use of space and its associations (community constrained mantel test; $p < 0.002$ for all days) was observed, and this correlation is maintained even after controlling for variation attributable to first-order relatedness (constrained partial mantel test; $p < 0.002$ for all days). In addition, no correlation between first-order genetic relatedness and space-use (mantel test, $p > 0.05$ for all days) was observed, suggesting genetic and spatial contributions to associations are independent. No significant differences across experimental conditions were observed after correcting alpha for multiple tests (Kruskal-wallis test; $\alpha = 0.0125$; $X^2 = 8.06$; $p = 0.045$).

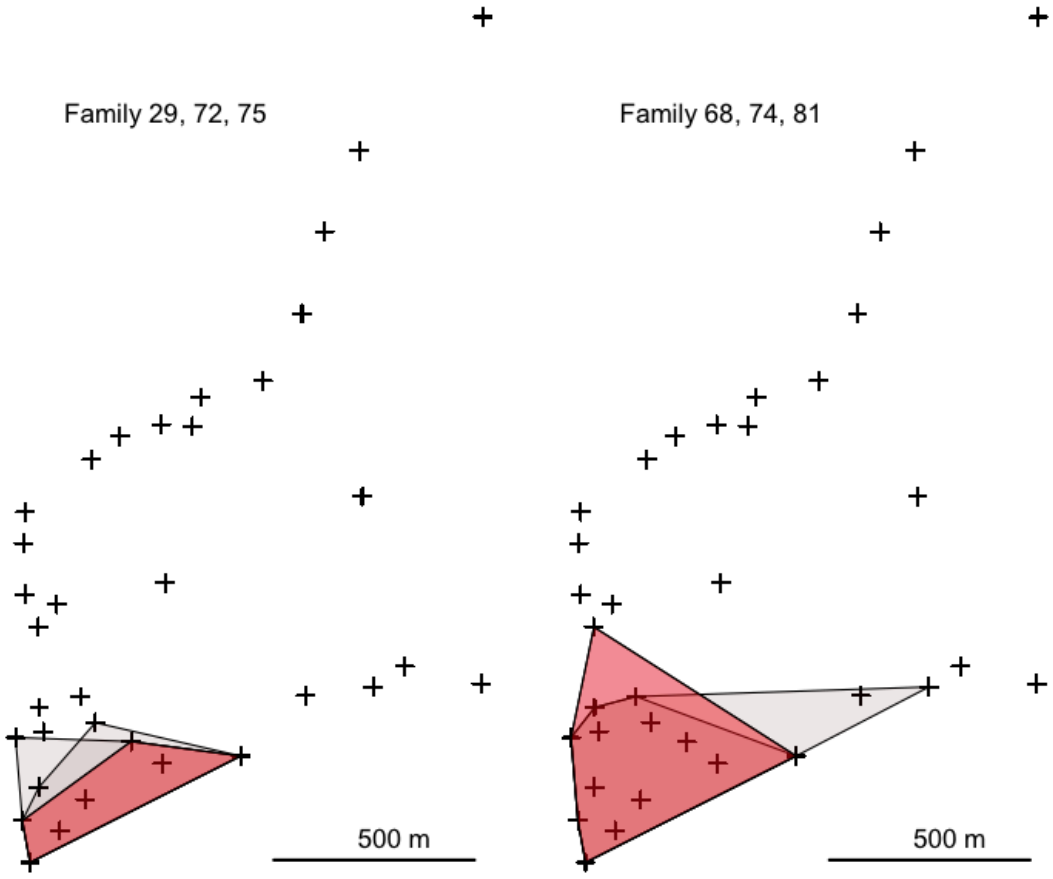

Figure 5. Home Range Overlap of two social families in the Southern community after 7 undisturbed days. Juvenile home ranges are depicted in red, with that of adults in grey. Each + is a base station that recorded whether or not the bird was in the vicinity. In family 29-72-75 (left), the home range of the juvenile is completely captured by the social family, whereas in family 68-74-81 (right) the juvenile has a section of unique space. In both cases, the juveniles share most of their use of the environment with their social family.

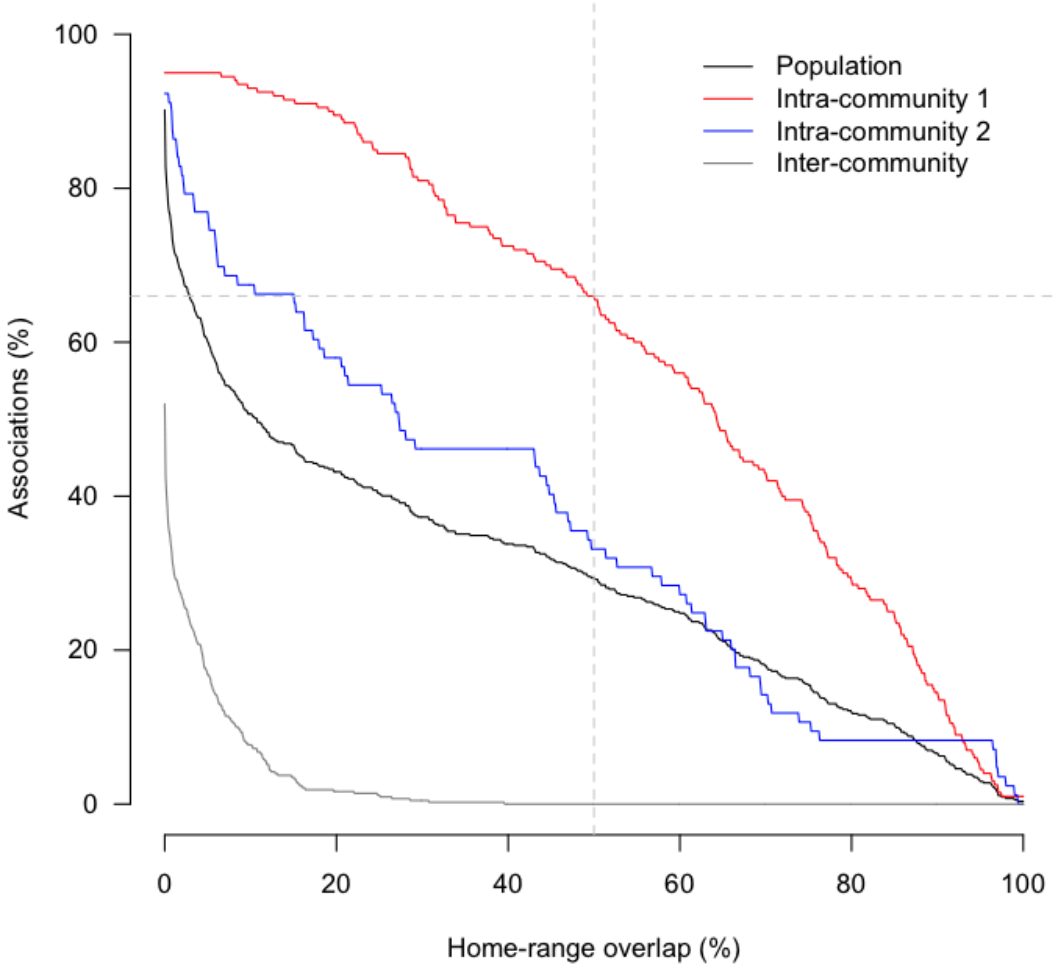

Figure 6. The number of associations that occur at a given percent home range overlap. The Northern community ('intra-community 1') had *ca.* 70% associations with more than 50% home range overlap (depicted by the dashed grey line), and the Southern community ('intro-community 2') has *ca.* 40% associations with more than 50% home range overlap. Birds from the two communities share a maximum of 40% home range overlap.

Discussion of Section 2

Throughout this section, I measured the social network through an animal-borne device that measured the proximity of two tagged NC crows through transmitted and received radio waves. I used the received power of each tag, rather than the calculated distance quantified in Section 1, to remind the reader that we interpret the received power as a proxy for distance.

I presented the first social network of wild NC crows, described correlates to their association through first-order relatedness and use of the environment through the use of their home-range overlaps. In Chapter 4 and Chapter 5, I revealed through an experimental manipulation that wild NC crows substantially increase their social partners and duration of encounters due to a community-centric food glut. In particular, I showed that the change to the network occurred between 5:00 and 6:00, and that NC crows increased their social partners during roosting. Moreover, in Chapter 7, I found that wild NC crows prefer inserted tools, suggesting that indirect information exchange via tool artefacts could facilitate the maintenance of tool use in a population. Finally, in Chapter 8, I uncovered that space-use not only drives potential direct information exchange, but also reveals the probability in which NC crows could encounter abandoned tools placed by conspecifics. Altogether, this section furthered our understanding of the lives of a difficult-to-observe wild corvid that uses and manufactures tools unlike most other animals.

CHAPTER 9

ANIMAL-BORNE TECHNOLOGIES AID GLOBAL DEVELOPMENT (TABLE OF CONTENTS) 210

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Animal-borne technologies aid global development

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Abstract

The 2013 United Nations Human Development Report highlights disease, hunger, and environmental degradation as hindrances of growth and development. An increasing body of evidence reveals that animal-borne technologies, devices attached to animals to measure their behavior, facilitate robust evidence-based policies to overcome these grand challenges. We examine the use of animal-borne technologies to inform global policy decisions governing conservation, food security, and public health; and argue for increased use of and funding for these devices.

Zoonic Challenges in Global Development

To develop successfully, nations must overcome numerous challenges, including protecting the diversity and richness of the world's fauna, ensuring wildlife conservation for tourism, preserving enough natural resources for human consumption, and monitoring and treating zoonotic diseases. Emerging infectious diseases (EID) place a heavy burden on global economies and undue strain on public health, and wildlife contributions to EID incidence has increased from 52% from 1990-2000 to 71.8% in 2008 [1]. Furthermore, infectious diseases transmitted from wildlife to livestock decrease the food supply, lead to significant economic losses, and trigger public outrage against wildlife [2]. On the other hand, wildlife is often an essential part of food consumption, especially in developing countries, with some estimates in Central Africa reporting that *c.a.* 579 million individual wild animals are consumed [2]. Moreover, protecting our world's flora and fauna stimulates eco-tourism, and increases globalized travel [3]. Thus, understanding the dynamics of human-wildlife-livestock

interactions will mitigate the burden of these grand challenges and stimulate increased development with comprehensive evidence-based policies.

Animal-borne Technologies

In an increasingly globalized world, complex interactions between wildlife, livestock, and humans are becoming commonplace [3], thus rendering good quality datasets essential for crafting effective public policies, especially within the developing world. Scientists have deployed animal-borne technologies on a wide-range of taxa, including mammals, birds, reptiles, fish, and amphibians, and in numerous environments from the pelagic seas to the tropical rain forests [4-8]. These studies collect high-resolution datasets and produce findings with global implications for conservation, food security, and disease transmission.

Conserving our planet's wildlife

Animal-borne technologies have been used to inform conservation efforts, and support development of eco-tourism by investigating animal behavior, space-use, and migration patterns (See Box 1, [6, 8-9]). In particular, animal-borne technologies shed light on numerous concerns for threatened species, from previously undetected mortality threats to uncovering novel reproductive biology [6, 8-9]. A radio-collar study found that predation and drought are responsible for mortality in adult endangered sonoran pronghorn (*Antilocapra americana sonoriensis*), while drought was the predominant cause of death in fawns [6]. Moreover, proximity sensing radio collars placed on Tasmanian devils (*sarcophilus harrisii*) revealed a single connected network

facilitating disease exchange directly or through conspecifics, suggesting specific management policies that target age or sex would have limited potential to prevent transmission of devil facial tumor disease and conserve this species [5]. In Namibia, radio-tracking cheetahs (*Acinonyx jubatus*), elephants (*Loxodonta africana*), lions (*Panthera leo*), and vultures (*Gyps africanus*, *Gyps coprotheres*, and *Torgos tracheliotos*) to understand their ranging behaviors has increased conservation efforts [8, 10-11]. Using this data, the Namibian government and private companies have increased the conservation of wildlife to spur development by investing in eco-tourism, with proposed expansion of up-market lodge operations at the Nyae Nyae Conservancy [3]. Participants of Namibia's Community Based Natural Resource Management program have documented benefits exceeding 1.1 million USD in 2002, and eco-tourism-related revenue generated in the Nyae Nyae Conservancy has been predicted to increase by 930% in 2015 from 100,000 USD in 2002 [3].

Protecting the food supply

Animal-borne technologies have further been utilized to inform food security by measuring wildlife and livestock interactions within a resource-finite setting, and determining the amount of wildlife or livestock available for consumption (See Box 1 and Box 2, [3, 8-9]). Competition between livestock and wildlife has been well documented, particularly in developing nations; therefore, greater understanding of the resources shared between wildlife and livestock yield policies reflective of the total ecological burden on resource availability [3]. Furthermore, wildlife consumption, when poorly or ineffectively regulated, can be unsustainable. For example, most

fisheries are fully exploited or overexploited, threatening the industry of small-scale fisheries and aquaculture and the employment of over 41 million people, of whom the majority live in the developing world [12]. Animal-borne technologies have been extensively used to develop sustainable fishing policies by providing in-depth knowledge of dynamics between fish populations and their habitats [7]. The Mekong giant catfish (*Pangasianodon gigas*) is one of the most important and high-value fish commodities in South-east Asia, but the wild population is critically endangered due to overfishing and river development [13]. Using sound waves to track location, acoustic telemetry has found that hatchery-reared immature catfish re-introduced into the Mekong river successfully migrate both upstream and downstream of the release point in the river, and may cross international borders from Thailand to Laos, suggesting the necessity for international cooperation for effective management and conservation of the species [13].

Mapping transmission of zoonotic diseases

Animal-borne technologies have been deployed to study transmission of infectious diseases, such as tuberculosis, West Nile Virus, Nipah virus (NiV), and avian influenza, from wildlife to humans, and from wildlife to livestock, which amplifies detrimental effects to local inhabitants (See Box 2, [4-5, 14-15]). Several outbreaks of NiV have been reported in Southeast and South Asia, killing 40-75% of those infected [4]**.** Flying foxes (*Pteropus vampyrus*) are important natural reservoir hosts of NiV, and recent research has documented NiV transmission from these hosts to pigs (*Sus spp.*) and humans [4]. Satellite telemetry quantified regular and seasonal movement patterns of

flying foxes, demonstrating that flying foxes travel between Indonesia, Malaysia, and Thailand, and are not deterred by large stretches of ocean, such as the Strait of Malacca [4]. These findings identify additional risk areas in the region for future NiV outbreaks, supporting the inclusion of flying foxes as a migratory species, and legislation that covers wildlife and disease management across national borders [4]. Moreover, with increasing concerns about a potential avian influenza pandemic, tracking wild bird populations using animal-borne technologies has begun to uncover essential information governing the migratory patterns, juvenile dispersal, and home ranges of these host species [4], which will inform policies to contain or prevent disease outbreaks.

The current state and future of animal-borne technologies

Animal-borne technologies are not limited to a single discipline: these devices are being deployed to address an increasing number of questions from conservation related eco-tourism to the human-livestock-wildlife interface. Currently, studies utilizing these devices have provided invaluable insight into disease transmission, ensuring the development of tourism industries in developing nations while monitoring conservation efforts, such as assessing fish stocks to ensure food security [4-8]. These devices are being increasingly improved from miniaturization of their internal components to development of better battery life. These improvements allow for longer deployments on smaller fauna across numerous environments to collect high-resolution datasets. Altogether, animal-borne technologies have the potential to translate real-world data into improved evidence-based policies, and in an increasingly globalized world, the

outcomes from studies performed in one region of the world yield insight to problems in another region.

Towards Public Policy

Our zoonic global challenges are best solved through scientific investigation, and we have already witnessed a steady change in many governments around the world implementing evidence-based policies. The most comprehensive methodology, collecting high-resolution evidence along with the use of the scientific method, ought to inform our public policy. With increasing calls across numerous fields of science, such as healthcare, management, livestock welfare, environmental sciences, and conservation, to implement evidence-based policies, legislators should increase funding for technologies that yield extensive datasets. Animal-borne technologies epitomize this notion, providing quality data to solve some of the world's biggest challenges. Thus, an effective use of scarce financial resources is to invest in sound scientific methods to lift the large burden on developing nations.

Box 1. Human-carnivore conflicts: Balancing conservation with food security

The rapid increase in the human population has been associated with greater consumption of and habitat loss for wildlife, resulting in increased conflicts with humans. Human-carnivore conflicts often arise from livestock depredation and result in retaliatory or preventative killing of these carnivores [8]. Human-carnivore conflicts have been documented in over 75% of all felid species [8]. Many of these carnivores include threatened or endangered species, such as cheetahs (*Acinonyx jubatus*), snow leopards (*Uncia uncia*), lions (*Panthera leo*), and tigers (*Panthera tigris*); therefore, conservation of these carnivores is a priority, especially for tourism [3, 8]. Contrarily, these carnivores represent significant financial losses to people working in livestock production. For example, lions are responsible for killing 1-2% of all livestock, and an annual economic loss of up to $130,000 in Cameroon's Waza National Park [8]. Moreover, livestock depredation due to leopards (*Panthera pardus*) results in a loss of 9% of family incomes in India [8]. Therefore, effective management policies need to navigate the complex balance between conservation and supporting livelihoods.

Recently, animal-borne technologies have been used to understand the habitat overlap between carnivores and humans to inform livestock management practices, that may lead to human-carnivore conflicts [8-9]. In Kenya, animal-borne technologies have studied the home-ranges of hyenas (*Crocuta crocuta*), characterizing temporal patterns of human-carnivore conflict [8]. In Northern Botswana, the endangered African wild dog (*Lycaon pictus*) is often persecuted for allegedly predating livestock. A GPS-collar study demonstrated that although wild dogs frequently travel within the vicinity of cattle posts and farms, they subsist mainly on small game, and are not largely

accounting for livestock losses, responsible for only 2% of predator attacks [9]. However, most of the wild dogs within the surveyed areas were killed within 3 months after the conclusion of the study, with only two adults known to have survived [9]. Unfortunately, there is a dearth of scientific information both on monitoring human-carnivore conflicts, and evaluating the consequences of management techniques with regards to both conservation and food security. Therefore, the use of animal-borne technologies can bring important insight to address the multi-faceted issue of human-carnivore conflict.

Box 2. Bovine tuberculosis: Connecting food security with zoonotic disease transmission

Bovine tuberculosis (*Mycobacterium bovis*) is a chronic zoonotic disease characterized by fatigue, poor appetite, weight loss, dyspnea, and cough, and is difficult to clinically distinguish from *M. tuberculosis*, the most common cause of human tuberculosis [15]. However, *M. bovis* is more likely to cause human extra-pulmonary tuberculosis than *M. tuberculosis*, and accounts for 10% of all human TB in developing countries [15]. Moreover, the 2010 World Health Organization reports that extra-pulmonary cases of TB increased by 116.6% in Tanzania between 1995 and 2009, suggesting that bovine TB is an increasing public health burden in the developing world [15]. Transmission of bovine TB between humans is rare; contracting bovine TB predominantly occurs from contact with infected animals or by consuming infected animal products [15]. Many people in developing countries depend on livestock for their livelihoods, with Tanzania having the third largest domestic stock population in Africa [15]. Unfortunately, proper inspection of the meat entering the markets is not effectively administered for numerous reasons, such as inadequate veterinary services, in developing countries [15]. Thus, better evidence-based policies to combat the spread of bovine TB are in great demand.

Animal-borne technologies have been used increasingly to understand disease transmission dynamics of *M. bovis* around the world, and these findings have important implications for public policy [5]. In particular, animal-borne technologies have determined that brushtail possum (*Tricosurus vulpecula*) population density positively correlates with transmission rates, and evidence further suggests that indirect

transmission in possum populations occurs [5]. Therefore, locations with higher populations of possums may be higher risk zones for disease transmission. Interestingly, a study deploying an animal-borne radio-collar demonstrated that African buffaloes (*Syncerus caffer*) migrate more under dryer conditions, increasing the transmission of bovine TB [14]. Given that global climate change is predicted to result in drier conditions in Africa, controlling the spread of bovine TB is essential to maintain the well-being of local inhabitants [14]. Further analysis of the data obtained by animal-borne technologies demonstrate that high prevalence of bovine TB in buffalo populations, suggesting that vaccination alone will not be an effective management tool in Africa [15]. The culling of host species, such as the badgers in Britain, can actually increase prevalence of bovine TB in cattle populations due to greater migration of the remaining host [15]. Thus, combining multiple strategies, including vaccinations, culling, and minimizing the movement of cattle, requires further exploration [15]; and animal-borne technologies could provide a wealth of data to answer the efficacy of a multi-avenue strategy.

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CHAPTER 10

The aims of my thesis were to explore the sociality of wild tool-using New Caledonian crows (NC crows; *Corvus moneduloides*) through the use of a novel technology, to characterize this new proximity device (*Encounternet*), and to experimentally test whether NC crows gathered information from tools left behind by conspecifics. Altogether, I 'reality mined', or explored every 20 seconds of each crow's social life, our dataset to understand the role of relatedness, an environmental manipulation, and space-use on the social patterns of these wild birds. Furthermore, I calibrated *Encounternet*, exploring its strengths and weaknesses. During this process, I also aimed to explore the implications of our findings with this technology, such as whether data should be trimmed *a priori* or *a posteriori*. Moreover, I sought to explore the use of animal-borne technologies in our species' largest challenges: food security, conservation, and disease transmission. Altogether, I have furthered our understanding of wild New Caledonian crows' sociality, and explored this novel method to extract information from a population of wild, undisturbed NC crows.

Summary and implications of findings

First, I explored *Encounternet*, a novel system developed at the University of Washington to enable 'scientist-to-tag-to-tag-to-basestation-to-scientist' communication, alongside the ability to program specific parameters, such as frequency of tag pulse, the number of pulses used to create each encounter record, and the number of successive pulses that the tags would miss before closing an encounter log. The key parameter recorded by *Encounternet* tags is the power at which a tag received another tag's pulse. Received power (RSSI) is a proxy for the distance between the sending and receiving tags. Therefore, we designed a comprehensive calibration exercise to convert received power to distance by building a physical model, collecting data *in situ*,

creating a mixed effects model from the physical model, parameterizing the model with the collected data, and simulating the probability a received power represented a distance. Simply, there was a lot of noise: converting received power to distance was not one-to-one. We uncovered that the height of the tag above ground was the largest factor contributing to error, with habitat and antenna orientation contributing to small differences in RSSI. Because of this noise, throughout my thesis, I presented RSSI value rather than distance to remain transparent about what exactly we were able to measure.

In **Chapter 3** of my thesis, after an inspirational conversation with Professor Emiel van Loon, we recognized the necessity for users of animal-borne technologies to follow a method to evaluate error of the animal-borne devices prior to deployment. After realizing that no studies have yet to outline a procedure to distill the quantitative process of error discovery into manageable steps, we developed a four-step method—*know*, *identify*, *evaluate*, and *store*. First, users of animal-borne devices should know or recognize the numerous factors that contribute to error in their devices. Next, a model ought to be created from physical principles and parameterized through data collected from the device. Then, evaluation of arbitrary parameters through sensitivity and uncertainty analyses to ensure the selection of parameters does not affect the outcome (or if they do, at least researchers would able to identify the limits of those parameters). Finally, the model and data should be stored for other scientists to use. After working with a single device to shape the manuscript, we broadened the scope of the paper to include most animal-borne devices, such as GPS, RFID/PIT tags, acoustic loggers, and accelerometers. In doing so, we aimed to convince our audience that our process to manage error would yield more accurate and transparent results. Principally, we wanted

to ensure that the limitations of the technology were considered when presenting the biological outcomes of interest.

Since the error of *Encounternet* tags was quantified, and distance probabilities could be assigned to RSSI values, we deployed the tags on wild tool-using NC crows. Thus, in **Chapter 4**, we produced the first network of NC crows, revealing more social partners than previously predicted (Holzhaider *et al*. 2011). Furthermore, we discovered two communities of wild NC crows, even though they were trapped only 1200 meters apart; detailed community analysis revealed core family units alongside numerous non-family connections. In addition, we uncovered that both adult males in a social family were not genetically related to the juvenile in the social family, suggesting that extra-pair copulation may be common in wild NC crows as has been observed in numerous bird species (for reviews, see Griffith *et al*. 2002, Westneat and Stewart 2003, and Akçay and Roughgarden 2007).

Further to these discoveries, in **Chapter 5**, we aimed to quantitatively understand the response of these birds to environmental heterogeneity through a food glut. To do this, we carried a large pile of candlenut wood infested with beetle larvae to an inter-community central location and two intra-community central locations. We detected significant increases in the number of social partners, the duration of time spent with conspecifics, and the number of individuals roosting together. Moreover, we monitored these responses after the experiment was removed, revealing 1) a return to baseline levels of the number of social partners, 2) a return to baseline for the Northern community in the time spent in association and an experimentally heightened duration in the Southern community, and 3) a heightened number of co-roosting pairs. In addition, we revealed a significant correlation between the genetics (first-order relatedness) and time spent in association during the baseline, which disappeared for

two days during the intra-community experiment, and returned after the experiment was removed. The loss of correlation highlights the removal of genetic barriers to potential information exchange due to environmental manipulation.

Both Chapter 4 and Chapter 5 focused on direct social transmission, thus I decided to investigate another potential pathway for information exchange, indirect, or space-use driven, tool-related associations. In **Chapter 6**, I established the preference of wild NC crows for vertical sticks over horizontal sticks resting on a foraging location, and further revealed that their preference is due to its insertion. In addition, I showed that the inserted tool preference is removed when an environmental cue, the product of the wood-boring beetle—sawdust, is placed on the same foraging location as the resting stick. I revealed that tool-properties, such as the selection of tool length or diameter (Chappell and Kacelnik 2002, Chappell and Kacelnik 2004), could have been exchanged in indirect social processes—or through the preference for inserted abandoned tools left by conspecifics.

To further explore whether the abandoned tools could play a role in the acquisition of tool-properties, I examined the use of space by these wild NC crows. In **Chapter 7**, using data collected from *Encounternet*, I analyzed the space-use of our population of wild NC crows, and revealed numerous home ranges that overlap. These results alongside the assumption that foraging could occur at any location indicates that the discovery of abandoned tools could be from a large number of other individuals and not just from the immediate social family. In addition, I revealed that juvenile NC crows use the same home range as their social family, thus the potential for a juvenile NC crow to discover an abandoned tool may be driven by the space-use of the adults in their social family. Furthermore, the preference for adults to use inserted tools combined with previous observations (and the quantitative home range discoveries

herein) of juvenile NC crows following their parents suggests that tool-properties are likely to be exchanged through unrelated NC crows, as the discovery by parent/adult NC crows (through stimulus enhancement) would facilitate the tool choice and deployment strategy of a conspecific to a juvenile NC crow. I also demonstrated that space-use is highly correlated with direct social information exchange, and that this correlation is preserved even when the genetic structure is accounted, suggesting that space-use and genetics independently control the probability of whom one encounters.

Having explored the sociality of wild NC crows, I combined the methods and biology sections to discuss, in **Chapter 8**, whether *a priori* or *a posteriori* filtering of data from proximity devices, similar to *Encounternet*, could miss biological outcomes. Having quantified the variation of received power at a given distance, and having experimentally manipulated the network with a pile of wood containing beetle larvae, I addressed whether the use of a single power filter was capable of missing an increase in social partners. I discovered that at a received power 10 decibels lower than our initial filter, an increase in social partners during the experimental time period could be observed, suggesting that proximity devices, such as *encounter* (Prange *et al*. 2006), that filtering incoming pulses by received power could miss biological outcomes. I recommend that using *a priori* filtering proximity devices necessitate switching either to a power setting such that *a posteriori* sensitivity analyses can be implemented or to collect all possible signals such that *a posteriori* filtering of all data can be undertaken. Importantly, numerous studies have deployed these tags using *a priori* filtering, and, we ought to re-evaluate their claims to ensure the presented results were not artefacts of the technology (for example, see Hamede *et al*. 2009).

Finally, due to my interest in science policy, in **Chapter 9**, I sought to address the use of animal-borne technologies in our understanding of global development.

While the core of this thesis focuses on information exchange in tool-using New Caledonian crows, the use of animal-borne technologies spans the range of scientific questions from disease transmission to conservation to food security. As such, I argue that governments ought to fund these technologies to collect the best evidence possible to inform their policies.

Altogether, I have quantified the genetic, social, and spatial lives of wild NC crows, demonstrated their preference for abandoned tools, improved our understanding of a new proximity device, *Encounternet*, and recommended the alteration of our methods to deploy proximity devices.

Sociality in wild New Caledonian crows

Three primary components must be investigated to understand the maintenance of tool-use in these birds: genetics, environment, and sociality (Cavalli-Sforza and Feldman, Richardson and Boyd and 2005, Odling-Smee *et al*. 2008). In the wild, these three factors influence one another; therefore, each factor could contribute to the acquisition of novel behaviors, such as tool-use (Cavalli-Sforza and Feldman, Richardson and Boyd and 2005, Odling-Smee *et al*. 2008). NC crows are suspected to transmit socially (culturally) and accumulate tool-related information, such as tool designs, the location of tool-use, and/or tool-properties (Hunt 1996, Hunt and Gray 2003, Holzhaider *et al*. 2010, 2011, Hunt *et al*. 2012). I (along with my co-authors) quantified NC crows' sociality, compared their sociality with relatedness, and manipulated the environment to see how genetics and sociality responded to this heterogeneity. Herein, I discuss the current state of our knowledge relating the genetic, social, and environmental context regarding the acquisition of tool-use, and improve our understanding in view of the results presented in this thesis.

Numerous qualitative observations have been published over the years, especially those discussing the social make-up, structure, and organization of these wild birds. Numerous observations (Hunt and Gray 2003, Kenward *et al*. 2004, Holzhaider *et al*. 2010, 2011, Hunt *et al*. 2012) have described a core family basic structure, though these observations lacked quantification. Herein, I quantified the home ranges of juveniles with their families and found that a juvenile's use of the environment was equivalent to that of its parents. In addition, I revealed that first-order relatedness was correlated with associations, suggesting that relatedness (in part) determines who associates with whom. However, the genetic results also suggest that a 'social' family is not necessarily the same as the 'genetic' family. We reveal that the adult male that formed a part of the 'social' family is not first-order genetically related to the juvenile, suggesting extra-pair copulation occurs in wild NC crows. In addition, these results suggest that future models of information flow ought to consider a discrepancy between the genetic and social make-up of vertical, or between 'parents' and 'offspring', transmission of information.

Comparing the genetic structure to direct and spatial associations allows for a critical assessment of a key parameter of information spread throughout a population: dispersal. Evidence suggests that juvenile NC crows socially acquire tool-use or manufacture (Kenward *et al*. 2006, Holzhaider *et al*. 2010), and between the first or second year, juvenile NC crows disperse, or leave from their family's general location (Holzhaider *et al*. 2011). To quantify dispersal distance, genetic relatedness is a useful tool to examine the differences between populations; I reveal that the community structure is not genetically divided, confirming previous work presenting the genetic structure of four unique populations (Rutz *et al*. 2012). Dispersal appears not to occur

over kilometers, as locations greater than 15 kilometers had a different genetic make-up, but those sites within a few kilometers were genetically similar.

Previous studies have qualitatively described the re-use of tools left behind by conspecifics (Bluff *et al*. 2010) or by juveniles re-using their parents' tools (Holzhaider *et al*. 2010). I demonstrated in **Chapter 6** that adult NC crows prefer an inserted tool to sticks resting on the foraging surface, suggesting that these tools could expose a foraging crow to foraging opportunities and the tool-choice of the previous user. My results suggest that while juvenile NC crows adopt the tools used by their social parents, their social parents are attracted to tools left inserted, and as I uncovered in **Chapter 7**, the previously inserted tools have a high probability of being from numerous non-first-order related individuals. Thus, while the parents, through stimulus enhancement (Holzhaider *et al*. 2010), passively facilitate juveniles' use the tools immediately thereafter; the adults' choices reflect the tool-properties of other NC crows. This chain of events leads to two suggestions: 1) the maintenance and selection of tool-properties could be driven by the re-use and re-exposure of tools from the population, and 2) while stimulus enhancement is the direct process that the juvenile is exposed to tools, the indirect process by which the tool was initially ascertained by the parents still facilitates the juvenile to acquire information through non-social family means.

A key question remains: does information spread vertically (from parent to offspring), obliquely (from non-related parent to juvenile), or horizontally (from juvenile to juvenile or adult to adult)? First, different types of social learning may play a role in the exchange of tool-related information (Holzhaider *et al*. 2011). All evidence to date suggests that vertical transmission is extremely likely, as related mothers and juveniles spend significant amounts of time together relative to non-related females

(Kenward *et al*. 2004, Holzhaider *et al*. 2010, 2011, Hunt *et al*. 2012, Chapter 5, Chapter 7). In addition, we discovered two adult males that were spending an equal amount of time as the related mother with the juvenile, suggesting that extra-pair copulation is occurring, and thus, oblique information exchange (unrelated, social family male) is also extremely likely. Interestingly, we find differing pieces of information for horizontal information exchange based upon age. First, adults prefer inserted tools, and thus encounter the tool-related properties and foraging choices of another (most likely) adult NC crow. Whereas, juveniles tend to follow parents and use tools *after* their parents use tools (Holzhaider *et al*. 2010, Hunt *et al*. 2012). Thus, horizontal exchange of information between adult NC crows seems likely; yet, we have no evidence to suggest horizontal information exchange between juvenile NC crows. Altogether, I demonstrated that the sociality of wild NC crows is not simple: vertical and horizontal transmission of information is possible through direct and indirect processes.

NC crow sociality compared to other corvids

Based on qualitative observations of NC crows at foraging tables, Holzhaider *et al*. (2011) stated, "the likely social network size of NC crows is small compared to that of many other corvids." The authors support this statement using two examples: 1) rooks can roost with hundreds of other pairs (Clayton and Emery 2007), and 2) pinyon jays live in permanent flocks of 50-500 individuals (Balda and Bateman 1971; Marzloff and Balda 1989). I take a more restrictive and conservative view when comparing the sociality of wild corvidae. Rather than placing NC crows on a spectrum from social to non-social, I propose we compare network structures, specifically discussing the relative network capacity by quantifying the number of associations that occur out of

those that could possibly occur. Importantly, this strategy moves beyond simply stating the raw number of individuals in a given location to the relative number of associations with those individuals.

The availability of resources is responsible for the carrying capacity of a given location (Pastor *et al*. 1997). Therefore, comparing the number of individuals with whom an animal could associate rather than the percent of individuals can be misleading. Simply, just because there are more individuals does not necessarily correspond to more For example, rook roosts can contain hundreds of individuals (Lewis 1995, Marzluff *et al*. 1996). While there are significantly more individuals, we can speculate on the structure of the roosts being non-random—certain individuals are likely to remain closer together on average, such as first-order related individuals or family units (Lewis 1995, Marzluff *et al*. 1996). As such, with restrictive distance filters similar to those of RSSI 15 (or within *ca*. 10 meters), we hypothesize that the percent of total individuals with whom a single individual is in association with is small. This is similar to NC crows' roost patterns, only roosting with a small percentage of those individuals present.

Pinyon jays live with between 50 and 500 individuals in undefended territories (Balda and Bateman 1971). Flocks were observed moving from location to location covering large blocks of land, yet quantifying unique individuals within the flock has yet to be done (Balda and Bateman 1971). Marzloff and Balda (1989) quantified a female-biased dispersal pattern in the pinyon jay, revealing that in scarce foraging conditions, flocks tended to become smaller and more nomadic. Thus, comparing NC crows with pinyon jays is confounded by the resource availability, with NC crows' food coming from both tool-use and non-tool use sources (Rutz *et al*. 2010).

Unfortunately, detailed networks of other corvids are not available for comparison. Preliminary social structures for ravens (*Corvus corax*) suggest that family units spend significantly more time together than with non-social family (Fraser and Bugnyar 2010). This similarity is promising, as ravens have been observed in the wild to use tools by dropping rocks on the heads of intruders attempting to gain access to their nests (Janes 1976). Thus, it could be possible that the tight family social structure is an adaptation or a predisposition to acquiring tool-using skills.

Exploring this concept leads us to recognize the numerous Corvids that have been observed using tools. 9 species in the genus Corvus (outside of NC crows) have been observed using tools in either the wild or captivity (for references, see Beck 1980, Shumaker *et al*. 2011).

Table 1. The common name, species, and location of observation (wild or captivity) of all known tool-using corvids.

Common name	**Species**	**Observed**
Pied crow	albus	Wild
Hooded crow	cornix	Wild
American crow	brachyrhynchos	Wild, Captivity
Northern ravens	corax	Wild
Fish crow	ossifragus	Wild
Rooks	frugilegus	Captivity
Fantailed raven	rhipidurus	Unknown
Northwestern crow	caurinus	Captivity
Indian house crow	splendens	Wild

Thus, exploring the sociality of these species and comparing their sociality to species of corvids not observed to use tools could reveal whether social structure is correlated with tool-use. Unfortunately, the social network of many of these species does not exist. Thus, future work comparing these species will begin to unravel the connection between tool-use and sociality.

Altogether, qualitatively comparing different species of crows to determine whether a social structure has evolutionary meaning remains in its infancy. With the adoption of animal-borne devices to record social networks, hopefully more networks of corvids will be measured. Quantitative comparison of sociality between species will provide insight into the evolutionary origins of some remarkable wild behaviors, such as tool-use.

Limitations

My thesis contains numerous limitations from technological to sample sizes to slow data collection. First and foremost, the use of radio waves to capture encounters between birds was much noisier than anticipated. Previous work demonstrated that other devices, such as GPS, have problems acquiring a signal under the canopy or in remote places, such as New Caledonia (Paul *et al*. 2005). In addition, a prospective paper described *Encounternet* as the future of our ability to capture wild animal behavior (Krause *et al* 2011). *Encounternet* is a noisy system, with the most important factor being height above ground; as such, I highly recommend future studies deploy proximity systems on animals that maintain the same height above the ground, such as zebras (See ZebraNet: Juang *et al*. 2002). However, we were able to quantify the variation introduced from environmental variables, and calculate uncertainty and robustness measures to ensure the technological error did not cause our biological

signals. As such, the detriment of high noise was mitigated by our ability to understand the error in our prediction.

Proximity devices only measure associations, or proximity to another individual, and say nothing about their behavior. While throughout my thesis I describe the ability for NC crows to exchange information, I limit this interpretation to the potential to exchange information, as we have no knowledge as to whether an interaction took place, and whether the interaction was agonistic or affiliative. Therefore, any and all mentions of behavior in studies using proximity devices must take into consideration that we only have data on time, location, distance between individuals, and the number of individuals in association.

We were only able to perform a single experimental manipulation; thus the implications from this single manipulation are constrained to explaining just this manipulation. However, the results of this experiment match our predictions, NC crows move towards food, and as a consequence to this movement, increase the time and number of encounters with other individuals. Moreover, had we run multiple experiments, we would have confounded our own experimental time periods, as some experimental measures, such as roosting partners, did not quickly return to pre-experimental levels. Thus, the latency effect was an unpredicted side effect of being forced to do a single experiment. Unfortunately, the inability to repeat was not in our control, after being forced to conclude this study with a bulldozer entering our site to further the development of the area.

Finally, the greatest limitation was the pure amount of data that can be generated with such a system. A commonly used phrase in the humanities is to 'reality mine' (Krause *et al*. 2013), or to measure the real-world decisions made by the operator. We measured association and space use patterns up to every five minutes and

every twenty seconds, respectively. A base station grid is unable to record a continuum of animal locations that a GPS device yields, which is still much too heavy to be deployed on passerine birds at this resolution; As such, I was unable to use more advanced spatial analyses, such as incorporating time into the space-use pattern to further our probability of encountering another's tools. Future deployments using more high-resolution techniques will also have large, high-resolution data, though perhaps statistics will become unnecessary, as the device will record every second of the animal's life (Krause *et al*. 2013).

Future directions

There are six items that I believe should be pursued in the future: three guiding principles and three experiments. The three guiding principles are: 1) the use of the framework to identify and quantify error in their animal-borne devices; 2) altering our use of *a priori* filtering technologies; and 3) recognize and increase funding for animal-borne technologies to inform global development policy. The three experiments, which I'll discuss more in detail below, are: 1) replication of our wild experiment and pursuing other forms of wild manipulation; 2) modeling information flow through the population and across the island of Grande Terre; and 3) an ontogenic experiment to test whether abandoned tools increase the acquisition of tool-use.

First, we were only able to undertake a single experiment, and while we were able to extract a significant amount of information, replicating this experiment would allow for more general conclusions. Specifically, replicating this experiment within and between habitats would reveal whether different populations of NC crows have similar responses to a food glut. In addition, this outcome would reveal the necessary results to map the spread of information through the population of NC crows, rather than just

understanding the response of dry forest crows to a tree-fall. Similarly, other types of experiments, such as removing a bird and quantify the response of the network to the loss of the bird, could yield worthy advances by enhancing our understanding of network responses to death or dispersal.

Second, to model information flow across the main island of New Caledonia, Grande Terre, certain pieces of information are necessary, such as number of social partners, genetic relatedness, dispersal patterns. I provided the first account of the duration and frequency in which wild NC crows associate and discussed dispersal patterns. Unfortunately, additional information, including a survey identifying the number of NC crows in New Caledonia, the population heterogeneities between rain forest and dry forest, is necessary to inform information flow, (from personal experience, when I visited the rainforest I only heard vocalizations from two birds, whereas in the dry forest, we captured *ca.* 25 birds at a single location). In addition, understanding the social learning capability of NC crows is essential, whether NC crows are capable and use simple mechanisms (*e.g.*, stimulus enhancement, social enhancement), more advanced mechanisms (*e.g.*, emulation, imitation), or none at all!

Finally, I would suggest that the ability to investigate the process by which abandoned tools facilitates the selection of tool-properties could transform our understanding of the maintenance and spread of tool-related information. Specifically, an experiment allowing one group of NC crows to have only access to inserted tools to perform a task (along with a third control group with no information), and comparing their success in foraging with a group exposed only to direct social information could reveal that the necessary information for tool-properties to propagate through a population may not require direct social influences.

To conclude, I believe the future is promising to further our understanding of tool-oriented behavior in wild NC crows. As technologies continue to improve, quantifying behavior and placing some previously described laboratory behavior back into nature will be a success. I hope I made a small contribution to our knowledge of this fascinating species; I must say that exploring and quantifying the intersection of 'behavioral evolutionary ecology' has been extremely exciting!

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APPENDIX 1

their mothers. While this might sound unpleasant for the mothers, their milky skin is specially modified for its role in rearing, and mothers are totally unhurt by their rapacious offspring. Although this maternal dermatophagy and extended parental care was only discovered very recently, it may be quite widespread in caecilians and appears to have been around for more than 100 million years.

What is interesting about these amphibians? Caecilians may be most interesting by virtue of their phylogenetic relationships. As their sister group, they are equally as important as Batrachia (all the frogs and salamanders put together) to any attempt to infer features of their common amphibian ancestors and the history of early terrestrial vertebrate life. For example, that all oviparous caecilians lay their eggs on land rather than in water makes it plausible that the last common ancestor of the living amphibians and that of all living tetrapods also practiced terrestrial oviposition. If so, the origin of the amniotic egg would have been preceded by a long history of terrestrial amphibian eggs.

Similarly, recent studies have revealed that frog and salamander skin secretions are rich in bioactive peptides with potential biomedical applications. Given their phylogenetic position, we might expect study of the slimy skin of any caecilian to enhance the known diversity of such compounds more than would study of any additional batrachian. As an independent lineage, caecilians provide many opportunities for comparative biologists to test theories on the evolution of diverse traits that were developed from studies of better-known taxa. For example, caecilian skin feeding and viviparity may provide useful analogues in the study of the evolutionary origins of lactation.

Why are there so few species of caecilians? Good question. Currently there are only about 190 species of caecilian that have been described, compared to more than 600 species of salamander and over 6000 species of frog. Given recent discoveries, the actual numbers of species in each of these groups are far from certain, although the apparent differences in the orders of magnitude in the species diversity of frogs compared to caecilians and to salamanders is very unlikely to change. Perhaps frog speciation rates have been higher because of their use of song in mate recognition and courtship, or due to occupancy of relatively diverse habitats. In contrast, caecilians have no vocal communication and mostly occupy a more homogenous environment. However, caecilians remain poorly studied taxonomically and many areas in which they occur have been very incompletely surveyed. An entirely new family and radiation of caecilians was found recently in northeast India and it seems entirely plausible that there could be at least twice as many species worldwide as are currently recognised.

I've heard there are global declines in amphibian populations, is that true for caecilians? There have been severe declines, and even extinctions, of some wild populations of frogs and salamanders in recent years. However, despite some anecdotes, there are no good data for caecilians. We do not know if caecilians are troubled by pathogenic chytrid fungus and the IUCN Red List compendium of conservation assessments lists just six caecilian species as threatened while the majority (66%) are 'data deficient'. This ignorance is no basis for being sanguine. Some caecilians seem well-suited to traditional agriculture in the tropics, maintain healthy populations in cultivated areas, and do not seem threatened. In contrast, less adaptable species may have already gone extinct due to changes in land use and large-scale habitat change must be considered a threat to caecilians as it is to many kinds of animal and plant.

Where can I find out more?

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Automated mapping of social networks in wild birds

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Growing interest in the structure and dynamics of animal social networks has stimulated major advances [1–3], but recording reliable association data for wild populations has remained challenging. While animal-borne 'proximity' tags have been available for some time [4], earlier devices were comparatively heavy, had limited detection ranges and/or necessitated recovery for data retrieval. We have developed wireless digital transceiver technology ('Encounternet') that enables automated mapping of social networks in wild birds, yielding datasets of unprecedented size, quality and spatio-temporal resolution. Miniature, animal-borne tags record the proximity and duration of bird encounters, and periodically transfer logs to a grid of fixed receiver stations, from which datasets can be downloaded remotely for real-time analysis. We used our system to chart social associations in New Caledonian crows *Corvus moneduloides* [5,6]. Analysis of *ca.* 28,000 encounter logs for 34 crows over a 7-day period reveals a substantial degree of close-range association between non-family birds, demonstrating the potential for horizontal and oblique information exchange.

New Caledonian crows use tools to extract prey from deadwood and vegetation, exhibiting remarkable behavioural sophistication [5]. The species is suspected to transmit tool-related information through cultural processes, with crows learning from each other how to make or deploy certain tool types [6]. Our biologging system overcomes difficulties of observing New Caledonian crows in their natural habitats [7] and enabled us to address two main objectives: to chart opportunities for social learning over a range of encounter distances; and to investigate whether social information is

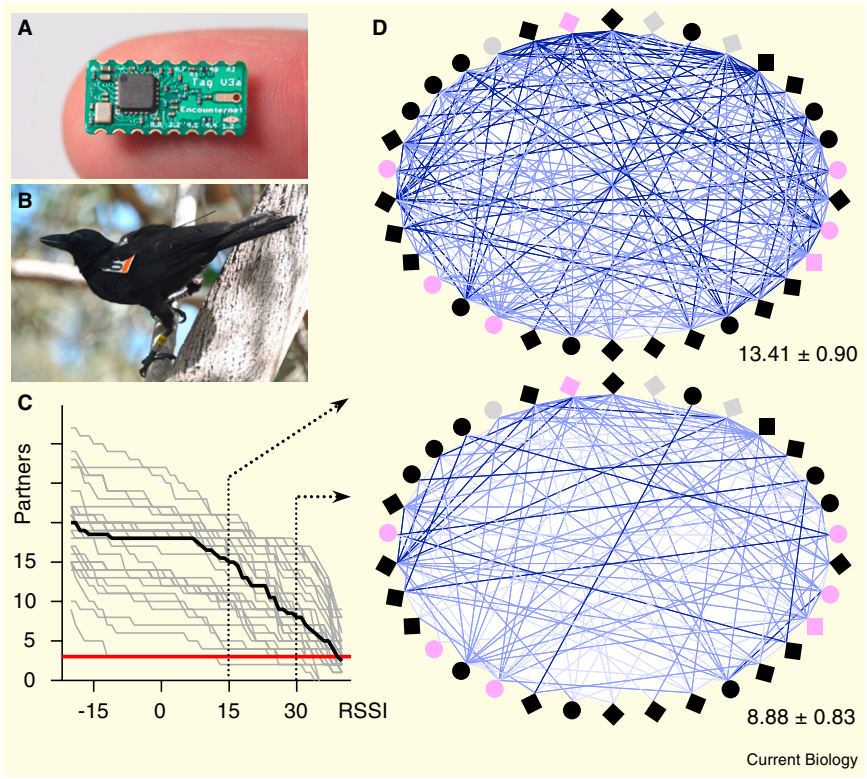

Figure 1. Automated mapping of social networks in wild birds.
(A) Miniature transceiver board with an ultra-low power microprocessor (<0.3 g; on the tip of an index finger for scale). (B) A wild New Caledonian crow with a harness-mounted transceiver tag. (C) Number of social partners ('node degree') as a function of minimum bird-to-bird distance (as measured by tag-recorded 'received signal strength indicator' values, RSSI; grey, *n* = 34 individual crows; black, median for network). The horizontal red line indicates the maximum degree expected if crows only associated with members within core family units (three), and vertical dotted lines mark the RSSI cut-off values used for generating sample networks. (D) Examples of a 'wide-range' network (edges represent at least one encounter of within *ca*. 21 m over 7 days; *top*) and a 'close-range' network (within *ca*. 5.5 m; *bottom*), with respective degree statistics (mean ± SE). In both cases, all birds are part of a single interconnected network. Nodes are arranged in random order on an ellipse (same for both networks) and coded according to sex (square, male; circle, female) and age (pink, juvenile; grey, immature; black, adult); edge 'weight' is shown in three increasingly dark shades of blue for (1), (2–9), and (≥10) encounter logs.

likely to flow between family groups — a process that may be essential for the effective cultural accumulation of innovations [8].

From 2 to 21 October 2011, we deployed miniature transceiver tags (9.57 ± 0.050 g, mean ± SE; Figure 1, Supplemental information) on 41 crows at one of our study sites in New Caledonia [7]. Tags were programmed to switch on synchronously after a 5-day cooling-off period, to allow the population to equilibrate after our trapping activities, operating thereafter on a 16-hour wake-time duty cycle (4:00–20:00 hrs). Active tags emitted ID-coded radio pulses every 20 seconds, whilst continually 'listening' for other nearby tags. Whenever two or more tagged crows came within detection range (usually several tens of meters), their tags recorded proximity data for their 'encounter' (as 'received signal strength indicator' values (RSSI), later allocated to distance classes using calibration data) in reciprocal date-, time- and ID-coded log files (Supplemental information). For sustained encounters, several pulses were combined into a single log file (covering a maximum of 452 seconds), providing minimum, mean and maximum RSSI values for analysis, and allowing an estimate of encounter duration (Supplemental information). Here, we use the shortest physical distance logged between crow dyads, derived from RSSImax, to chart opportunities for social learning. Since our technology cannot record the biological context of tag-recorded encounters, we refer here to 'encounters' or 'associations,' rather than 'interactions' [2,3] (integration of miniature video cameras could overcome this limitation; Supplemental information). A fixed grid of 45 tree-mounted 'basestations' was used to harvest data from roaming tags in the study area and to monitor the locations of tagged subjects (detection range usually *ca*. 100 m; Supplemental information). For *ad-hoc* network analyses, fieldworkers regularly downloaded data from basestations, working at night to avoid disturbance. While our system generated association data for *ca.* two months, we focus here on the first seven days, during which the network was entirely undisturbed. In this time period (>90 daylight hours), we accumulated, for 34 crows, some 28,000 unique bird-to-bird association logs and some 190,000 bird-to-basestation logs. It would have been impossible to generate datasets of comparable spatio-temporal resolution and information content with conventional techniques (Supplemental information).

Our technology uncovered a dynamic social system. While crows can gather some social information over larger distances, close-range bird-to-bird interactions may be necessary for the transmission of specific tool-related information [8]. We show that rich association patterns were present both in 'wide-range' networks, with encounter distances of up to *ca*. 21 m, as well as in 'close-range' networks, containing only encounters of within *ca*. 5.5 m where direct observation of tool-oriented behaviour would be feasible (Figure 1D). Notably, over a wide range of minimum encounter distances, birds had many more social partners on average (Figure 1C) than would be expected for crow families of 3.22 ± 0.22 individuals (*n* = 9 families) [9], indicating greater potential for horizontal and oblique transmission processes than previously inferred from observations at artificial feeding sites [9]. Although some dyads were only weakly associated, and many encounters will have occurred in non-foraging contexts, the fact that most birds consorted so widely within just a few days illustrates considerable scope for information flow in crow populations. Our study sets the scene for detailed analyses of the roles of individual animals, and network topologies, in driving the diffusion and diversification of cultural information in wild animal societies [10].

Encounternet will be useful in a wide range of contexts to obtain a comprehensive record of dynamic

animal associations. The technology is suitable for long-term deployment on relatively small animals, and overcomes key constraints of other data-collection methods. Importantly, with its high sampling rates and excellent tag-to-tag detection range, Encounternet can generate time-resolved association data needed to link network topologies to biological processes — a key challenge in social network analyses [2,3].

Supplemental Information

Supplemental information including experimental procedures and two figures can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.06.037.

Competing Interests

Encounternet was conceived and developed at the University of Washington, Seattle, USA, and BO, JBu and JBo are currently working on the technology's commercial exploitation.

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Wingless virgin queens assume helper roles in *Acromyrmex* leaf-cutting ants

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Division of labour is the hallmark of advanced societies, because specialization carries major efficiency benefits in spite of costs owing to reduced individual flexibility [1]. The trade-off between efficiency and flexibility is expressed throughout the social insects, where facultative social species have small colonies and reversible caste roles and advanced eusocial species have permanently fixed queen and worker castes. This usually implies that queens irreversibly specialize on reproductive tasks [2]. Here, we report an exception to this rule by showing that virgin queens (gynes) of the advanced eusocial leaf-cutting ant *Acromyrmex echinatior* switch to carrying out worker tasks such as brood care and colony defence when they fail to mate and disperse. These behaviours allow them to obtain indirect fitness benefits (through assisting the reproduction of their mother) after their direct fitness options (their own reproduction) have become moot. We hypothesize that this flexibility could (re-)evolve secondarily because these ants only feed on fungal mycelium and thus could not benefit from cannibalising redundant gynes, and because queens have retained behavioural repertoires for foraging, nursing, and defense, which they naturally express during colony founding.

Permanence of caste is the most fundamental difference between eusocial and cooperative breeding [2]. Helpers of the latter category may become breeders later in life and thus retain full flexibility towards the eventual pursuit of direct fitness. Illustrative examples are cooperatively breeding birds, paper wasps and some Ponerinae ants [3–5]. Workers of eusocial ants and honeybees, by contrast, at best retain some phenotypic plasticity for adopting specific behaviours depending on their age and the needs of the colony [6], but their reproductive potential is always permanently reduced. The behavioural repertoires of queens tend to be limited to mating, colony founding and egg-laying, and this never changes in response to queen condition. This should imply that gynes — unmated virgin queens —should be cannibalized or otherwise disposed of when they somehow fail to disperse on a mating flight, similar to infertile diploid males [7,8]. Uselessness for both colony-founding and altruistic behaviour means that failed queens have zero fitness and might thus be even expected to die voluntarily, as recycling of their tissues and prevention of further consumption of scarce resources will offer them at least some indirect fitness when their resources will benefit properly endowed siblings.

We observed field colonies of the leaf-cutting ants *Acromyrmex echinatior* and *A. octospinosus* that contained several non-inseminated wingless gynes besides the mother queen (Supplemental Information published with this article online). As these queens had been allowed to live, we hypothesized that they might still be worth their keep if they would assume helper roles that were of value for their colony. To test this hypothesis, we experimentally removed the wings of normal gynes and quantified worker-like behaviours. As controls, we used both completely un-manipulated gynes, and gynes with one middle leg removed. This mutilation was not expected to affect normal behaviour as queens missing a leg are occasionally observed as functional colony mothers.

Acromyrmex gynes with their wings experimentally removed were more likely to conduct worker tasks: unlike the control gynes, they took care of brood that we introduced into experimental nests (Figure 1A,B) and they attacked non-nestmates (Figure 1C). A second nestmate recognition experiment, in which tethered gynes were presented with nestmate or non-nestmate odour, showed that both the control and wingless gynes were equally able to discriminate between nestmate and non-nestmate cues (Figure 1D).

SUPPLEMENTAL INFORMATION

Automated mapping of social networks in wild birds

Christian Rutz, Zackory T. Burns, Richard James, Stefanie M. H. Ismar, John Burt, Brian Otis, Jayson Bowen, and James J. H. St Clair

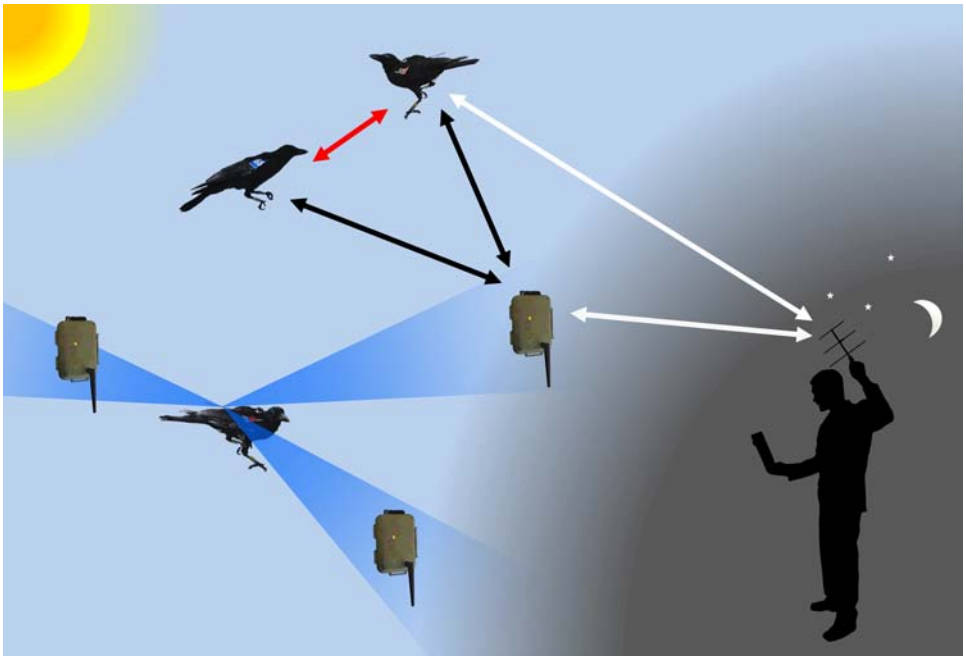

Figure S1, related to Figure 1. Schematic illustration of the rationale and basic operation of the 'Encounternet' system.

Bird-mounted transceiver tags transmit individual identification (ID) codes at a programmed pulse rate, whilst continually 'listening' for signals from other tags. When two or more tagged birds come within detection range (usually several tens of meters), their tags record proximity data for the 'encounter' (as 'received signal strength indicator' values, RSSI) in reciprocal date-, time- and ID-coded logs (red arrow). Meanwhile, whenever tagged birds come within the detection range of 'basestations' (usually *ca.* 100 m), basestations request stored log files from tags and initiate data download, clearing tag memory after successful transfers (black arrows). In addition, basestations log the presence (and RSSI) of transmitting animal-borne tags, so 2D (or even 3D) tag coordinates can later be established through cross-triangulation (indicated by blue triangular shading). Fieldworkers use 'masternodes' to download data wirelessly from basestations or tags, and to communicate with field-deployed hardware as necessary (white arrows), working at night to avoid disturbance to the study system. For example, masternodes can be used to reprogram devices (e.g., resetting of tag pulse rate or duty-cycle parameters), to calibrate hardware clocks for system synchronisation, and to track birds manually in the field through cross-triangulation and homing-in. Note that the schematic is not drawn to scale and that not all possible communication routes between tags, basesations and masternode are shown.

Figure S2, related to Figure 1. Wireless digital transceiver system for the automated mapping of social networks in wild birds ('Encounternet').

(A) Main hardware components of the Encounternet system: miniature transceiver tag, fully packaged for deployment, as used in this study on New Caledonian crows (*bottom left*); autonomous receiver station ('basestation;' opened to show board and D-cell batteries, *bottom middle*, and closed ready for field deployment, *bottom right*); and portable controller unit with 3-element Yagi antenna ('masternode;' *top right*), plugged into a standard 10-inch netbook (*top left*). (B) A basestation deployed in the field. Suspending basestations in the crowns of tall trees, as far away from foliage and large branches as possible, significantly increases tag-to-basestation detection range. (C and D) A wing-tagged wild New Caledonian crow with a harness-mounted transceiver tag. The harness has a 'weak-link' on the breast strap (not visible in the photos) that gradually degrades and safely releases harness and tag after several months. The photos show the same bird (ring code VV2), on 19 October 2011.

Supplemental Experimental Procedures

Wireless transceiver system

Our system ('Encounternet') consists of three self-developed hardware components (Figure S2A): (*i*) miniaturised, animal-borne transceiver tags; (*ii*) autonomous field-deployed receiver stations ('basestations'); and (*iii*) portable controller units with 3-element Yagi antennae ('masternodes'). All hardware is controlled by custom software. The rationale and basic operation of Encounternet is illustrated schematically in Figure S1.

While animal-borne transceiver tags have previously been deployed on mammals (e.g., 'proximity tags' by Sirtrack Ltd., NZ; [S1]), these devices: were too heavy for smaller-bodied species such as flying birds (without collar, *ca.* 20–30 g; collar-mounted, *ca.* 120–500 g); had limited tag-to-tag detection range (*ca.* 30–100 cm, and at best a few meters); and/or needed to be recovered for data download (e.g., [S2–S5]; other systems: 'ZebraNet,' [S6]). Encounternet overcomes these problems, as well as key constraints of other techniques for recording animal association data, including direct observation, mark-recapture protocols, VHF radio-telemetry, GPS tracking, or RFID/PIT systems.

Our tags are small, lightweight, fully programmable and sufficiently energy-efficient for long-term deployment (weeks to months), yet achieve excellent data sampling rates (up to *ca.* 120 proximity detection records per minute), tag-to-tag detection ranges, and onboard data storage (up to 4,000 logs). Two-way communication between all three hardware components (Figure S1) ensures: that mapping of dynamic associations is not spatially constrained (as is the case with systems in which tags only transmit to fixed receiver stations, but not to other roaming tags; [S7,S8]); that animal movements can be tracked in 2D or even 3D space (through basestation cross-triangulation); that tag data can be downloaded wirelessly, either via basestations or directly using a masternode, for 'real-time' analysis (without the need to recapture animals or to recover tags); and that the system can be reprogrammed during field deployment (e.g., to remotely reconfigure tag settings including pulse rate and duty-cycling, or to synchronise tag and basestation clocks). In summary, we believe our project marks the technological breakthrough in recording animal social network data that has been anticipated by several recent reviews [S9–S12].

Over the last few decades, biologists have developed a wide range of innovative packaging and attachment techniques for biologging devices, offering wide taxonomic scope for the application of our Encounternet technology. Apart from being suitable for avian applications, as described here, tags could be attached to leather collars or plastic ear-markers, for mounting on mammals, or designed to be glued non-permanently to reptile skin. As with any other biologging application, configurations need to be assessed on a case-by-case basis, and despite wide applicability, our tags may be unsuitable for certain species, because of either methodological and/or ethical constraints.

Encounternet has a modular design and can serve as a platform for collecting and transmitting other sensor information. We are currently working on the integration of accelerometers, microphones and GPS receivers, and hope to add video cameras and neuro-amplifiers in the future. Encounternet tags with onboard video cameras (*cf.* [S13,S14]) will ultimately enable researchers to distinguish 'interactions' from mere 'associations' – a long-standing challenge in the field of animal social network analyses (see main text and [S9,S10]).

Tag settings and calibration

Tag parameter settings can be tailored to maximise overall system performance, given known study objectives and constraints. We chose a pulse rate for our tags (one ID-coded radio pulse every 20 seconds, at 433 MHz) that comfortably exceeded the anticipated time scales of fission-fusion events in our crow study system (minutes to tens of minutes), and therefore enabled robust description of biologically meaningful association patterns. Tags 'opened' encounter logs when two birds came within signal detection range (i.e., recorded the timestamp of the first received pulse), and 'closed' logs (i.e., recorded the timestamp of the last received pulse) when either signal contact had been lost (for more than 120 seconds) or a programmed limit of 300 seconds had elapsed (firmware bugs caused *ca.* 58% of logs to exceed this limit; however, *ca.* 95% of logs lasted less than 340 seconds, while the maximum recorded log duration was 452 seconds). Successive logs were created during extended encounters (see previous note), ensuring that there was no upper limit to recordable encounter length. Proximity information was recorded as 'received signal strength indicator' values (RSSI), which in

our system are a measure (in integers ranging from *ca.* –20 to +50) of the power ratio (in dB) of the received signal, referenced to one milliwatt. Each encounter log contained a value for each of $RSSI_{min}$, $RSSI_{mean}$ and $RSSI_{max}$. Analyses reported in the main text and Figure 1 are based on $RSSI_{max}$ values (see below).

As will be described in detail elsewhere, we conducted extensive *in-situ* investigations to characterise the performance of our Encounternet system before deployment. An important objective of this work was to generate calibration data, so that tag-recorded RSSI values could later be converted into robust estimates of tag-to-tag/bird-to-bird distances. To this end, we used a fixed array of 12 or 18 tags, each mounted on a dead quail, to run a total of 24 trials, of 15 minutes each, across the five main habitat types in our study area. The resulting calibration dataset enables partitioning of observed RSSI variation into the following variance components: (*i*) tag-to-tag distance; (*ii*) habitat; (*iii*) tag height above ground; (*iv*) relative antenna orientation between tag pairs; and (*v*) residual, unmeasured sources of error.

Networks presented here are based on the presence of dyadic encounters within certain distances as determined from $RSSI_{max}$, with edges weighted according to the number of encounter logs (see below). Multiple encounter logs may result either from repeated independent encounters, or from fewer protracted ones. It is beyond the scope of this paper to distinguish the roles of encounter frequency and duration in determining association strength, but this can be achieved with our dataset by using encounter start- and end-times to calculate encounter durations (integrating across consecutive encounter logs where necessary), and using a refined RSSI-distance calibration fit (weighted according to estimates of crow habitat use and relative antenna orientation) to ascribe a distance, and appropriate confidence interval, to each encounter according to its RSSI values.

Basestation grid

For autonomous data collection, and spatial tracking of tagged birds, we tree-mounted (see Figure S2B) 45 basestations in our study site, with semi-regular spacing along the creeks of two convergent valleys (median nearest-neighbour distance was 93 m, with a range of 59–454 m). Basestations were deployed at above average density (and were programmed to download data only from detected tags that contained ≥ 60 logs) in

central areas of high suspected crow activity, and at comparatively lower density (and with a lower download threshold of ≥ 18 logs per detected tag) near the periphery of our study site, to maximise the grid's efficiency at harvesting data from crow-borne tags.

Trapping, tagging and crow attribute data

We used meat-baited whoosh nets [S15] to trap crows non-selectively at four different trap sites in our dry-forest focal study area (Taro and Tabou valleys of Gouaro-Déva; 21°33' S, 165°19' E), on the central west coast of Grande Terre, New Caledonia, South Pacific [S13,S16,S17]. Trapping started on 2 October and ended on 21 October 2011 (pre-breeding and early breeding season) when all traps were removed from the valleys. Diminishing returns from our trap sites, combined with re-sightings of tagged crows, suggest strongly that our sample of 41 tagged birds represented a substantial proportion of the local population, despite the fact that local crow density appears to have increased since earlier work [S17].

Following established protocols, all trapped birds were weighed, measured, and marked with rings and wing-tags [S13,S16,S17]. Encounternet tags were deployed on crows using individually adjusted weak-link harnesses ('one break–all release' design, 1.5-mm braid for large individuals, and 1.2-mm braid for smaller ones; Sirtrack Ltd., NZ; Figure S2, C and D). In an earlier VHF radio-tracking study (unpubl. data), this attachment technique was found to have no observable effects on crow behaviour (subjects habituated very quickly to harnesses and tags) and to release tags reliably and safely after several months; another research group also uses the same harness design for deploying VHF radio-tags on New Caledonian crows [S18]. We chose battery and potting options that ensured that tags had the same dimensions as our earlier, well-tolerated VHF radio-tags, and were so light (9.57 g ± 0.050, 8.90–10.21 g, n = 41; mean ± SE, range) that tag mass was only 3.35% ± 0.062 (2.65–4.07%) of crow body mass, which is well within the range of 3–5% recommended for avian biologging applications [S13,S19,S20]. Harnesses were *ca.* 1 g (small) and *ca.* 2 g (large), respectively, but because body straps were trimmed considerably during the fitting process (individually for each crow), final mass added was significantly lower, and in no case resulted in a combined tag-and-harness mass exceeding the safe limit of 5% of a subject's body mass. For further discussion of ethical considerations, and data indicating excellent

survival of tagged crows in our earlier biologging projects, see [S13,S14]. All tagging procedures and field techniques were approved by Oxford University's local ethical review committee (LERC approval granted 22.09.2009) and all relevant local authorities in New Caledonia (permits N°1341-2010/ARR/DENV and N°1886-2011/ARR/DENV; Direction de l'Environnement, Province Sud).

We used 'sex' and 'age' as attribute data for our network nodes (see Figure 1D). Birds were sexed using established molecular techniques (see [S15]; all analyses conducted in R.C. Fleischer's laboratory, Washington DC, USA), and age was inferred from gape colouration, which typically changes from pink to black during the first few years of life (scored as described in [S16]; see also [S21]).

Data collection and processing

The key objective of the present study was to chart potential routes of information transfer in a wild population of New Caledonian crows (see main text). Since this required data from a completely undisturbed group of birds, we applied strict protocols for data collection. Tags were programmed to switch-on at 4:00 hrs on 27 October 2011, to allow all tagged crows—and the population and social network as a whole—five full days to recover from our trapping activities before data collection commenced (during this cooling-off period, heavy construction machinery drove through one study valley briefly in the early morning, and again in the afternoon, but this is unlikely to have affected crows for more than a few minutes; in any case, this traffic ceased before system activation). After the system 'went live,' we visited the study site only at night (i.e., after sunset and before sunrise)—to download logs from basestations, to recalibrate tag clocks and to check tags' log memory (see below)—avoiding any disturbance to the study system. Additionally, present analyses are restricted to the first seven days of data collection, as we subsequently conducted a series of field experiments that caused local perturbation.

After downloading raw log files from basestations, we conducted several checks to ensure data quality. First, we included only birds in our analyses which had, for all seven study days, contributed data from sunrise to sunset, and which had been confirmed to be actively roaming in the study area, i.e., their tags had been recorded by multiple basestations throughout the study area (34 tags fulfilled these criteria; 3 tags

had substantially drifting internal clocks, resulting in incomplete data; 4 tags were never recorded, and were either faulty or deployed on birds that had left the study site). Second, for the resulting set of 34 birds, we discarded all data from before sunrise and after sunset (so that networks described activity during daylight hours, and not roosting associations). A frequency distribution of all logged $RSSI_{max}$ values (across the range of values used in this paper) exhibited unexpected 'troughs' at 22 and 28, and a 'peak' at 25. These anomalies, which are likely attributable to hardware (chipset) properties, do not affect the conclusions of our study.

To assess whether our basestation grid effectively collected data from roaming tags, we conducted two separate analyses. First, examination of basestation data demonstrated that all 34 birds visited many basestations during the study period (across seven days, the median number of different basestations visited per tag ranged between 8 and 11), with only 5 of 238 tag-days (2%) having zero basestation contacts. Second, our nightly checks of crow-borne tags (see above) revealed that tags only ever contained a small number of logs (usually between 100 and 300 logs, with a recorded maximum of 514 logs) and never approached memory capacity, confirming that birds regularly came within reception range of basestations and successfully uploaded their data. Taken together, these *post-hoc* system evaluations indicate that both the basestations' spacing and sensitivity settings were unnecessarily conservative.

Network analyses

To generate sample networks based exclusively on encounters in which crows approached each other to within known distances, we filtered our quality-checked dataset according to RSSI cut-off values. Inspection of raw calibration data (see above) which were collected under the most 'favourable' signal-transmission conditions (tags positioned 4-m above the ground with their antennae oriented in parallel), showed that even under these optimal circumstances, only 2.1% of all pulses received from a distance of 21 m had an RSSI $\geq$ 15 (n = 14 of 670 pulses), and only 5.5% of pulses received from 5.5 m had an RSSI $\geq$ 30 (n = 26 of 471 pulses). Accordingly, we applied an RSSI $\geq$ 15 'filter' (i.e., retaining all logs with $RSSI_{max} \geq 15$) to obtain a dataset for a 'wide-range' network, and an RSSI $\geq$ 30 filter for a more restrictive 'close-range' network (see Figure 1D). On average, pulse transmissions between bird-mounted tags

will occur in less-than-optimal conditions, so the use of our calibration data was extremely conservative and most recorded associations will have been over considerably shorter distances than indicated by our cut-offs. While our technology does not currently permit firm inferences about the biological context of tag-recorded encounters (see above and main text), it is known that New Caledonian crows tolerate other (family and non-family) individuals nearby during tool-use foraging, and rarely express overt/territorial aggression [S17,S18].

After this filtering step, encounter logs (counts pooled across all seven deployment days) were converted into association matrices using R [S22]. Reciprocal entries (bird A → bird B; bird B → bird A) were similar across the whole matrix, with some inevitable deviations (*cf.* [S23]). We symmetrised all final association matrices by using the larger of the two values throughout, as we had no reason to believe that these maximum readings were systematically biased. Edge weights were generated by assigning encounter-log frequencies to one of three bins: high (≥ 10 logs), medium (2–9 logs), or low (1 log); unlike many other field methods, our technology enables the establishment of 'zero' edges with high confidence [S9]. We consider single encounters to be important, given our objective of charting the full range of bird-to-bird social learning opportunities, and our relatively brief study period.

The network parameter of interest in the present study is mean 'node degree,' i.e., the average (or median) number of social partners per crow in our undisturbed, naturally admixing study population (see Figure 1C). For the following reasons, conclusions drawn from this measure are robust to possible methodological issues. First, with respect to our sample of tagged crows, informative analyses require only: *(i*) the inclusion of multiple local crow families; and (*ii*) that birds were trapped non-selectively and were therefore representative of the wider population (both of these conditions were fulfilled; see Figure 1C and above). Thus, the reduction in sample size from 41 to 34 birds, for example, is unproblematic. Second, with respect to our sample of association data, our study is certainly more likely to underestimate, rather than overestimate, node degree, because: (*i*) this measure increases with time (every study day produced a representative description of association patterns, but, as expected, novel dyadic associations continued to be formed as the study progressed); (*ii*) tag recording errors, or any other forms of data corruption, are more likely to result in the

loss of true associations than the creation of false ones; and (*iii*) our tags could only record encounters with tagged subjects, so any encounters with untagged crows do not contribute to our summary statistics.

We used UCINET [S24] for basic network analyses, and manually confirmed key results for node degree. Weighted networks were drafted in NetDraw [S25] and subsequently edited in graphics software, showing two node attributes (sex and age; see above). To facilitate visual assessment of node degree and edge weights, as well as comparisons between networks, nodes were arranged in random order on an ellipse, with the same order used for both sample networks (see Figure 1D).

Author Contributions

CR conceived, planned and lead the study, and secured funding; BO, JBu and JBo conceived and developed the Encounternet technology, and are currently working on its commercial exploitation; adaptations for field deployment in New Caledonia were designed by JBu, CR and JSt-C; JBu built basestations and masternodes, and JBu, JSt-C, CR, ZB and SI built tags; CR and JSt-C coordinated fieldwork; CR, JSt-C, ZB, JBu and SI designed protocols for field deployment; CR, JSt-C, ZB and SI conducted fieldwork; ZB managed the database and processed raw data, with support from RJ, JSt-C and CR; CR, JSt-C, ZB and RJ conceived and designed analytical approaches, which were then implemented by ZB and RJ; JSt-C, CR and ZB produced figures, using photos by JSt-C and JBo; CR wrote the manuscript, which was edited by JSt-C, ZB and RJ, and approved by all co-authors.

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APPENDIX 2

Eye dominance is correlated with lateralized tool-use in New Caledonian crows

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Abstract

New Caledonian (NC) crows (*Corvus moneduloides*) have been shown possessed of a wide binocular visual field that has been suggested to facilitate their use and aim of tools. However, revisiting the geometry of tool-use in ecologically relevant contexts shows that the majority of tool-use must necessarily be under monocular control. Furthermore, the NC crows show strong individual laterality in their tool-use, yet no functional explanation or correlation with other lateralities has been examined. We studied the correlation of tool laterality and eye dominance in 13 captive NC Crows. By assessing eye dominance *vis a vis* first investigative look in a task that forces monocular observation, and determining each individual's tool laterality, we demonstrate that an individual's eye dominance is correlated with the lateralization of its tool-use. This stands in contrast to the uncorrelated laterality of humans, likely a result of the anatomical constraints of tool holding in NC Crows, and suggests that lateralization of tool-use in the NC crows may result from the monocular nature of tool-use in hollow foraging and the necessity of holding a tool such that it can be aimed with the dominant eye.

Introduction

New Caledonian (NC) crows demonstrate the most sophisticated tool-oriented behavior amongst birds [1, 2, for a review, see 3], having been shown in lab settings to manufacture tools appropriate to problems presented [4], use up to 3 tools in logical sequence [5, 5a], and possibly attend to the functional properties of their tools [6; however see 7]. Moreover, NC crows have been shown, individually, to consistently hold tools on one side of the bill during use [8, 9, 10]. However, no functional explanation for the lateralized use of tools in NC crows has been explored.

Previous research [10] has established the NC crows' distinctly wide field of binocular vision when compared to other closely related corvids, and suggests that it is this wide binocular field, which uniquely allows the tip of a tool to lie in the visual field of both eyes (see Figure 1a), that underlies their success in tool use. The same study, however, shows that the NC crows shift from holding the tool straight to holding it lateralized as probing holes become smaller, allowing the eye ipsilateral to the tool shaft a straight line of sight to the probing target (see Figure 1b). While the study rightly emphasizes the necessity of a wide binocular field to allow the tool tip to land in the field of the shaft-ipsilateral eye, the probing holes used to investigate binocular tool use are larger in diameter than the foraging hollows typically encountered by the NC crows in the wild [11]. Revisiting the geometry of the crow's tool use for ecologically relevant probing hole sizes reveals the monocular nature of tool-use in hollow foraging and provides a potential functional explanation for the consistent lateralization of tool use.

As can be seen in Figure 1c, using average morphological measurements for α and β from Kenward *et al* (2004), and constructing the most conservative model (*i.e.* placing the eyes as far forward and narrow as possible, at the bill base, to maximize the depth that the contralateral eye can see into the hole), during normal tool use the contralateral eye cannot see the tool tip or probing target, the result of it's angle to the probing hole. The maximum depth visible to the shaft-contralateral eye, B, varies with the diameter and depth of the hole, as well as the distance from beak tip to the hole's opening, A. Only in cases for which this maximum depth, B, is greater than the depth of the target will binocular viewing of the target be possible.

Figure 1d plots each of these three variables for maximum depth and shows the ranges for which binocular viewing is possible (that is, those for which the maximum

depth of contralateral vision is greater than the hole depth). The Graph further shows the ecologically relevant ranges for hole depth and diameter, based on observation of the foraging hollows the NC crows' encounter in the wild [11]. The range for typical bill distance from hole reflects the range of tool lengths typically employed in the wild, as well as the personal observations (ZB and AK in the wild, AMIII, AMPvB, ZB, and AK in captivity) that the NC crows very rarely if ever engage in lateralized tool use at bill distances greater than 150mm. As can be seen, the overlap of the binocular range and the typical range is minimal, and only for the shallowest and widest of the typically encountered foraging hollows, and uncommonly large bill to hole distances is binocular vision of the probing target possible. Concordant with the observations of Troscianko *et al.* (2012), narrow holes require monocular control, and binocular control, at least once the tool is in the hollow being foraged, is not generally available to the NC crows in an ecologically relevant setting. This being the case, it is possible that the large binocular overlap of the NC crows' visual field is not itself necessary for successful tool use, but could instead be an artifact of the need for each eye's monocular visual field to extend far enough across that sagittal plane to include the tip of a laterally held tool.

With successful tool use thus predicated on monocular control, a potential functional explanation for the NC crows' individual consistency of tool-use side becomes apparent, namely eye dominance. NC crows' lateralized tool use is often compared to handedness in humans or manual preference in other primates [for example, see 9], but eye dominance, or the preferential use of one eye, also bears on one's ability to use tools. In humans, eye dominance and handedness are uncorrelated [13], as tools requiring fine-gauge aim may be held in the dominant hand and aimed with the dominant eye, whichever they may be. For species that manipulate tools with the extremities, this lack of correlation is not surprising, yet, not all tool-using species'

anatomy allows for this free combination of lateralities. In NC crows, which lack this degree of freedom in laterality, eye dominance could be a potential functional explanation for the observed individual laterality of tool-use.

Because of the anatomical constraints of holding a tool in the bill, only the eye ipsilateral to the tool shaft can look directly down the shaft, and therefore control aim of the functional end. It is critical here to note that because the avian brain lacks the interhemispheric integration of the mammalian brain (specifically, lacking a corpus callosum and featuring a near complete separation of the two visual pathways), monocular tasks represent a particularly strong lateralization of information in the brain [14]. Thus the NC crows' tool laterality serves to constrain visual awareness of the probing target to the eye ipsilateral to the tool shaft, and results in this eye controlling tool-use independently. Given this constraint, we would expect that the eye ipsilateral to the tool shaft is the NC crow's dominant eye, and that the laterality of tool use is itself a manifestation of eye dominance, with the NC crows referencing tool holding on the side that allows the dominant eye a straight view down the tool shaft.

Here, using the NC crows' 'first investigative look,' we examine whether their eye dominance is correlated with lateralized tool-use, possibly contradicting findings in humans [13], and offering a functional explanation of tool-use laterality as an outcome of eye-dominance and the inherently monocular nature of tool-use.

Materials and Methods

Subjects and housing

Subjects were 13 wild caught NC crows, all of which had been used in previous experiments. Birds were housed in groups of 2 or 3 in outdoor aviaries (60 m^2) with indoor enclosures (8m^2) accessed through an elevated door, with *ad libitum* access to

food for 12 hours per day and water at all times. Further details on housing conditions may be found in von Bayern *et al.* (2009).

Tool Laterality Test

Testing for tool laterality followed the method established by Weir *et al.* (2004), except where otherwise noted. We used a semi-circular section of tree stump as a probing apparatus. Two holes were drilled in the side, 1.6 cm in diameter and 10 cm deep. A length of dowelling 0.3 cm in diameter and 20 cm long was furnished for use as a tool (See Figure 2a).

Testing occurred before the usual food supply was placed in the indoor aviary each morning; *ca.* 11 hours after *ad libitum* food had been removed the previous night. The apparatus' probing holes were filled partly with chilled mealworms, with an additional mealworm placed near the opening of each to attract the birds' attention. The surface of the apparatus was sprinkled with sawdust to approximate the cues left by the NC crows' natural prey [16]. The apparatus was placed in the enclosure approximately 10 cm from the center of a wall with the tool placed perpendicularly 10 cm in front of the apparatus. A bird was confined to the indoor enclosure after placement of the apparatus, with all visual stimuli from the outside aviary blocked. Sessions were video-recorded from above the apparatus and lasted 30 minutes from the time of presentation.

Laterality of tool-use was scored in 'bouts' as described in Weir *et al.* (2004). A new bout of tool-use was defined as any time the bird changed tool grip or released the tool and moved its head before re-grasping it. Bouts were scored as 'right' or 'left' according to the cheek against which the non-functional end of the tool rested (see Figure 2c). Bouts were scored as 'straight' if the tool was held with the non-functional end in the bill. A bird was considered to have satisfactorily completed the test if it

engaged in a minimum of 10 lateralized bouts. If the bird did not achieve a minimum of 10 lateralized bouts, it was retested once and the bouts from both trials were summed. Individual lateral bias was determined via binomial test.

Eye Dominance Test

Birds that completed the laterality test were submitted to the eye dominance test. Eye dominance was determined via a *tube test* administered in the birds' indoor enclosure. The testing apparatus consisted of a rectangular wooden board (15.5 x 21 cm) with an opaque, plastic tube 8.5 cm in height and 1.6 cm in internal diameter protruding from the center (See Figure 2b). The tube was baited with a live darkling beetle larva (*Zophobas morio*), and the board around the tube was sprinkled with sawdust and mealworms to attract the attention of the bird [16]. The apparatus was placed in the enclosure approximately 10 cm from the center of the wall. A bird was confined to the indoor enclosure after placement of the apparatus, with all visual stimuli from the outside aviary blocked. All tests were video recorded from above the apparatus.

The birds' eye dominance was determined by the bird's first 'look,' to normalize analysis across all birds. First look was chosen as a reasonable assay of eye dominance, as most of the birds made only one look, ascertaining the problem and then seeking a cached tool ore attempting to upturn the tube to access the prey. A look was defined by one eye being placed directly above and within the bill's length of the tube opening (See Figure 2d), ensuring a direct and uninterrupted line of sight to the tube bottom.

Sessions lasted a minimum of 5 minutes and a maximum of 30 minutes, and ended *ca.* 5 minutes after the first look. If a bird retrieved a previously cached tool and approached the apparatus before making its first look, the tool was removed from the

enclosure once dropped and testing resumed. Each bird tested was subjected to sessions until it produced a first look, or until it had failed to do so in 4 sessions. If no looks were recorded after 4 sessions the bird was excluded from analysis.

Results

We tested 13 adult NC crows, 7 of which were female. 10 individuals completed the laterality test, of which 3 were right- and 7 were left-biased, adding more evidence to suggest that there is no population-level laterality as stated in Weir *et al.* (2004) and Rutledge & Hunt (2004). Individual laterality was determined excluding center-held bouts, as in Weir *et al.* (2004). Of these 10, 9 completed the eye-dominance test, of which 4 were right- and 5 were left-biased. The side on which the non-functional end of the tool was held was significantly correlated with the dominant eye ($n = 9$, two-tailed binomial test, $p = .039$). Only one bird that completed both tests showed the opposite correlation (see Figure 3, Table 1 in appendix).

Discussion

We observed a correlation between individual tool laterality and eye dominance, contradicting the non-correlation of lateralities observed in humans [13]. Only one bird that completed both tests held a tool consistently on the side opposite the dominant eye, and it should be noted that the one anti-correlated bird had the highest proportion of center-held tool-use bouts (see Figure 3). Furthermore, of the eight birds with correlated tool-use side and eye dominance, only one, Tumulte, engaged in any bouts of tool-use on the contralateral side, and these were far fewer that those on the ipsilateral side. Of the nine birds, 6 were left- and 3 right-lateralized, a result similar to that of Rutledge & Hunt (2004) and Weir *et al.* (2004), with no statistically significant population-wide

laterality. Eye dominance also showed no population wide laterality, with 5 birds exhibiting left eye dominance and 4 right.

Our results suggest that NC crows consistently hold a tool to the side of their face ipsilateral to the dominant eye to allow this eye to aim the tool in foraging hollows. This confirms the prediction made by our geometric model, that only the ipsilateral eye could properly see the probing target. The NC crows' consistent use of the tool shaft ipsilateral to their dominant eye suggests that this aiming function is preferred over depth perception, which would likely be controlled by the eye contralateral to the shaft [10]. Previous research suggests that the NC crows have a strong tactile feedback mechanism for perceiving depth [16]. It is likely that eye dominance evolutionarily preceded tool-use, as eye laterality is linked to other physical tasks in birds [17]. Cooptation of the dominant eye for tool aim may have resulted in selection for the tactile feedback mechanism, as birds with good aim and good tactile feedback would have been more successful foragers. However, we note that this study does not directly address the evolutionary selection of these behaviors

Our study is limited by a still-developing understanding of the neurological underpinnings of eye dominance. While we believe our assay of 'first investigative look' provides one assessment of eye dominance, our study is limited to correlation and does not directly test the mechanisms of laterality. However, in the context of non-correlated eye and hand laterality in humans and in human tool-use, the correlation of eye dominance with tool-use laterality in NC crows may suggest a functional explanation for this consistent laterality. The anatomical constraints of holding a tool in the bill inhibit the free combination of lateralities: there is no way for a contralateral eye to look down the tool shaft, so holding the tool contralateral to the dominant eye must come at the expense of losing its superior aim. The same is not true of handedness and

eye dominance in humans - objects can be manipulated with the dominant hand relative to either eye. Eye dominance, unlike handedness, does not exhibit population level laterality in humans, and it may be the case that population level laterality is only possible amongst freely combining lateralities. An investigation of another, non-tool-oriented laterality in NC crows that lacks the anatomical limitations of tool-use could further support this notion. Footedness, which has been shown to be lateralized across tasks in Japanese jungle crows, *Corvus macrorhynchos,* [17a], offers one such potential. A final caveat that must be raised is that while our results confirm the necessity of each eye's visual field to extend far across the sagittal plane, resulting in an abnormally large binocular field, we do not explain how this wide binocular field came about in the NC crows or whether it evolved as a by-product. Further behavioural tests would be necessary to establish whether NC crows are able to utilize their large binocular fields for stereoscopic depth perception, hence for gauging distances during tool use [10, 18].

The visual system in birds is a particularly rich area for investigation of laterality. The nearly complete lack of inter-hemispheric integration of visual information in the avian brain means that eye occlusion can have a dramatic effect on behavior [For example, see 17]. Visual information, at least in the immediate timescale, is not available to the contralateral brain hemisphere [14]; hence, occlusion isolates the covered eye's entire visual pathway from the presented task. As tool-use in ecologically relevant foraging hollows is a monocular task, occlusion of the dominant eye would likely elicit a switch in tool holding side, as the NC crows would have to position the tool shaft ipsilateral to the available, non-dominant eye. If tool laterality is indeed a function of eye dominance, we would predict that occlusion of the dominant eye would have a greater detrimental effect on tool proficiency than the non-dominant eye. One potential method to further explore the dominance of one visual pathway in tool-use

would be fMRI imaging of the birds' visual pathways during bouts of lateralized, occluded tool-use following the methods of [19]. This could potentially confirm a stronger reaction to tool-use problems for the dominant visual pathway.

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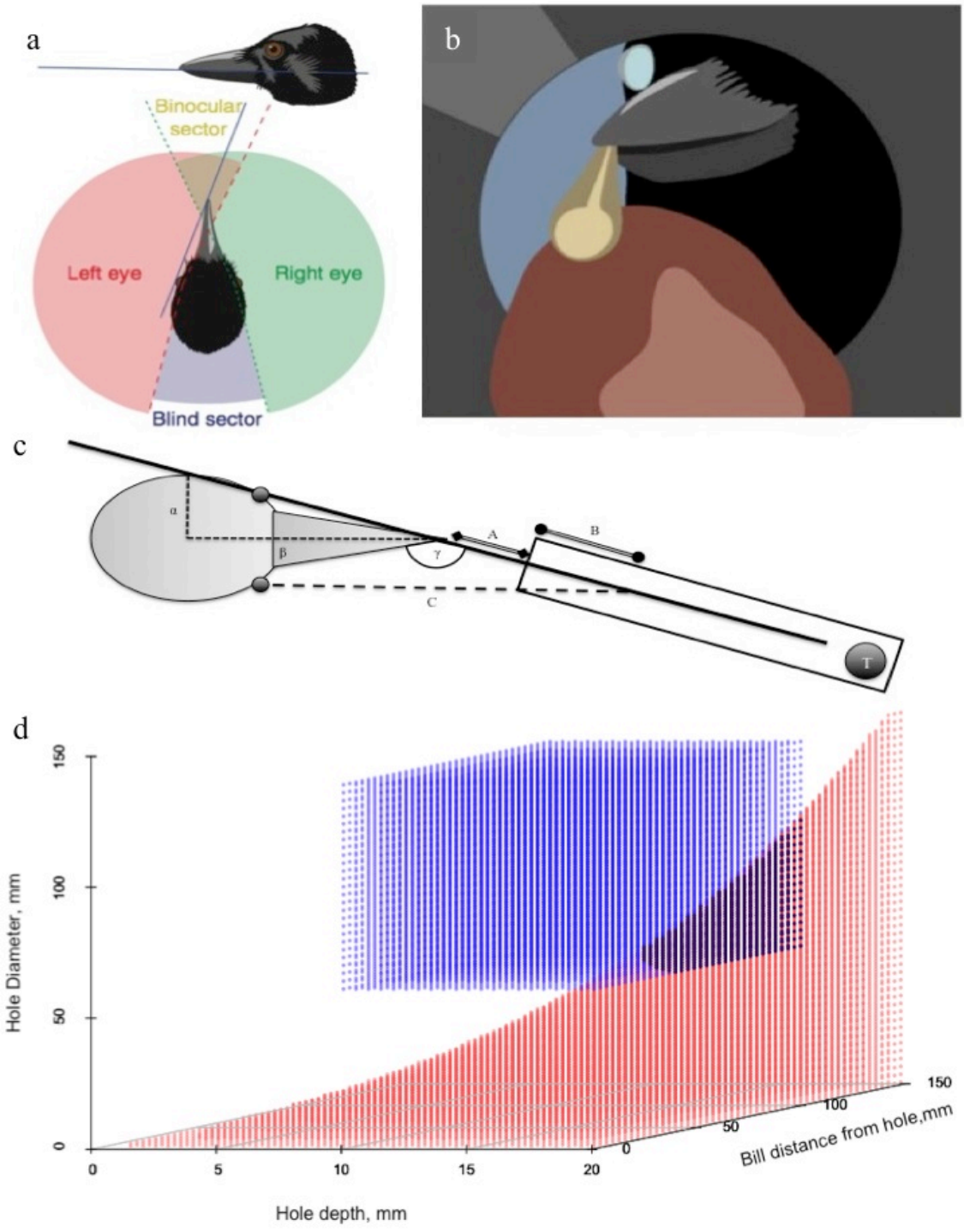

Figure 1. Image credit for (a) and (b): Dr. Joylon Troscianko, adapted from Troscianko *et al.* (2012) with permission from author. NC crows' perspective of a laterally held tool. a) The entirety of a left-held tool lies in the visual field of the left eye. b) The tool tip and probing hole in a right-held bout is reflected in the right eye, demonstrating its perspective down the probing hole. c) Demonstrates the limitations of tool viewing

during use by the eye contralateral to tool shaft. Using mean population morphology from Kenward *et al* (2004) for α and β, the angle of tool use, γ, can be calculated and used to determine the angle and depth at which the contralateral eye's deepest line of site, C, into the hole meets the tool. As distance 'A' decreases, distance 'B,' the maximum depth of tool visibility decreases non-linearly. For a typical A of 0-2cm, B can be no greater than 3.2cm. For a typical total length from tool tip to bill tip of 10cm, the tool tip and probing target, T, are not visible to the contralateral eye for any B < 5cm. (Trigonomic calculator in R available on request.) d) Graph of foraging hollow dimensions for which binocular viewing of target is possible. The light grey points represent the ecologically common foraging hollow sizes for the range of bill distances from the hole possible during probing for a laterally held tool of typical length. The dark grey points represent all combinations of hole dimensions and bill distances for which binocular viewing is possible. The black points show the overlap of these categories. As can be seen, binocular viewing is possible for typical holes only in a very shallow, large diameter minority of cases, and for high bill distances – uncommon in typical lateralized tool use.

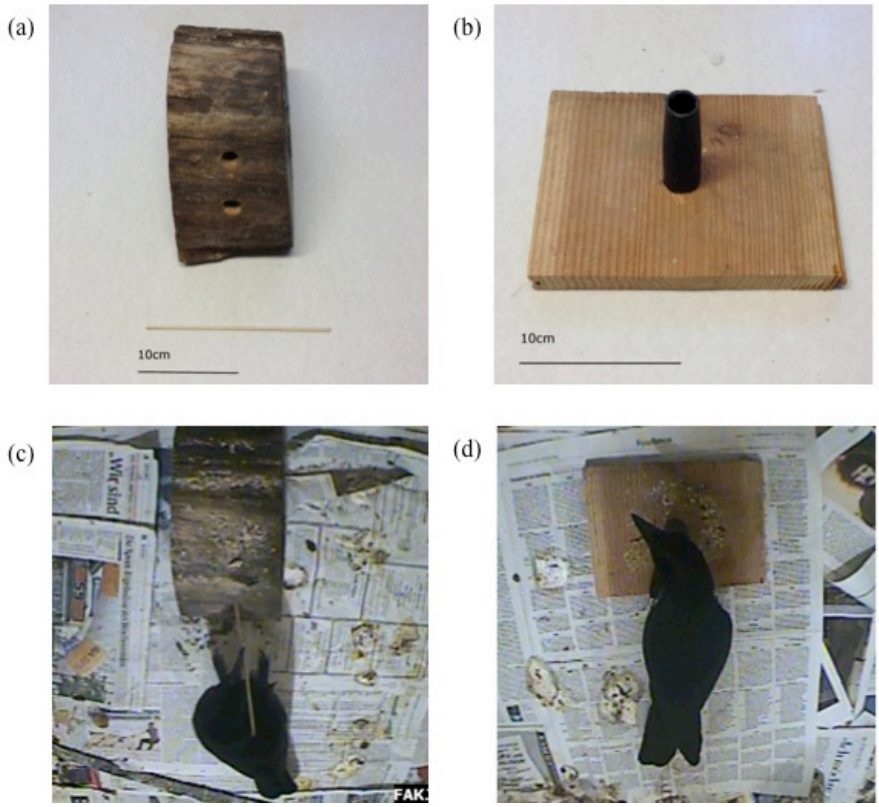

Figure 2. Laterality testing methods. a) Tool laterality probing apparatus and tool. Note the perpendicular placement of the tool to prevent approach bias. b) Eye dominance apparatus. c) A bout of right-sided tool-use by *Mango*. d) A right-eye 'look,' with eye placed directly to the hole, by *Liane*.

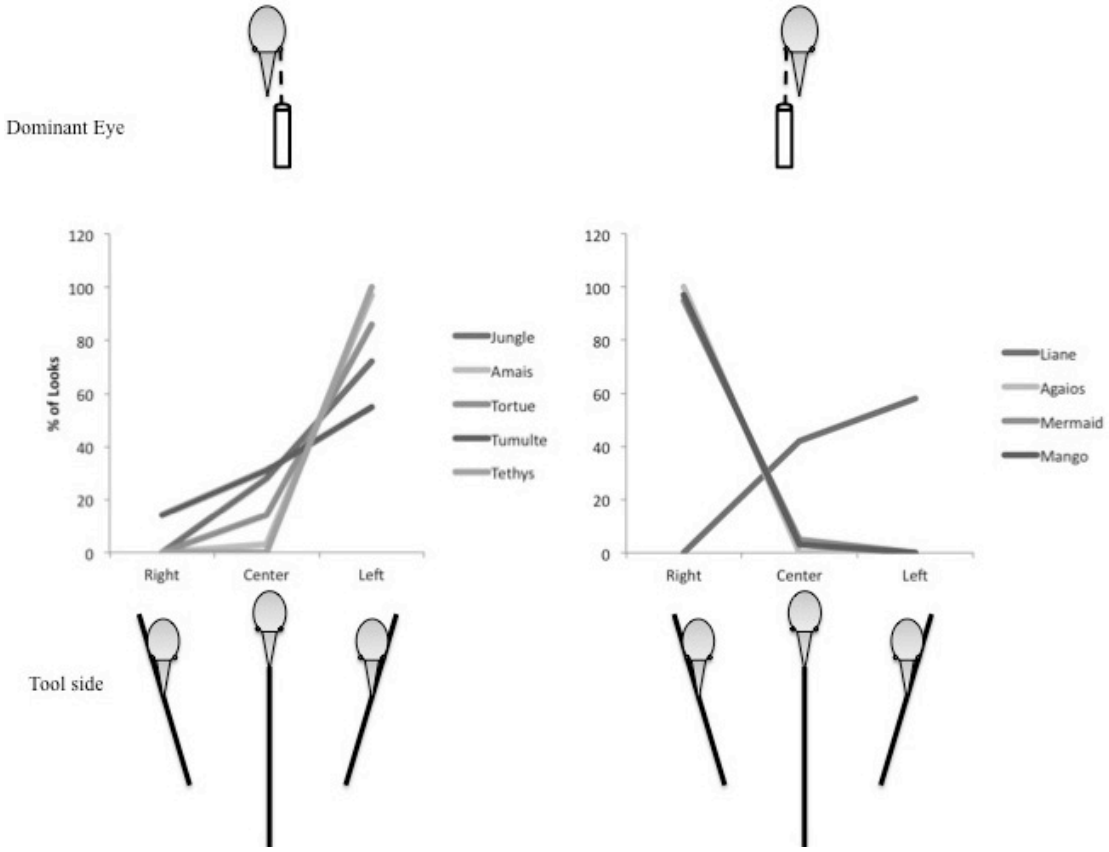

Figure 3. Percentages of tool bouts with respect to eye dominance. Each line represents an individual bird, showing the overall preference to hold tool on the same side as the dominant eye. Liane, the sole uncorrelated bird, can be seen on right, running opposite the trend. Note in particular her high percentage of center-held bouts. Also note that bird diagrams reflect a view from above, so left and right are switched.

Supplementary Online Material

Table 1. Correlation of tool laterality and eye dominance. Tool laterality was assessed via two-tailed binomial test, with all birds lateralized with $p < .001$. Of 9 birds, 8 consistently used a tool held on the same side as their dominant eye. *Bird completed tool laterality test in 2 sessions. **Bird completed eye dominance test in second session. ***Bird failed to provide tool-laterality. ****Bird provided tool laterality but failed to provide eye dominance.

	Tool Laterality					**Eye Laterality**	
Bird	Sex	Left Bouts	Center Bouts	Right Bouts	Tool Laterality	First Look	Correlated?
Jungle	M	18	7	0	Left	Left	Yes
Liane	F	19	14	0	Left	Right	No
Amais**	F	72	2	0	Left	Left	Yes
Agaios	M	0	0	42	Right	Right	Yes
Mermaid**	F	0	2	40	Right	Right	Yes
Tortue	F	12	2	0	Left	Left	Yes
Mango	M	0	0	47	Right	Right	Yes
Tumulte*	F	41	23	11	Left	Left	Yes
Tethys*	F	18	0	0	Left	Left	Yes
Birds Excluded for Unsuccessful Trials							
Coralie***	F	9	0	0	Fail	NA	NA
Cpt. Hook****	M	18	9	0	Left	Fail	NA
Titan***	M	1	0	6	Fail	NA	NA
Mangroove***	M	0	0	0	Fail	NA	NA