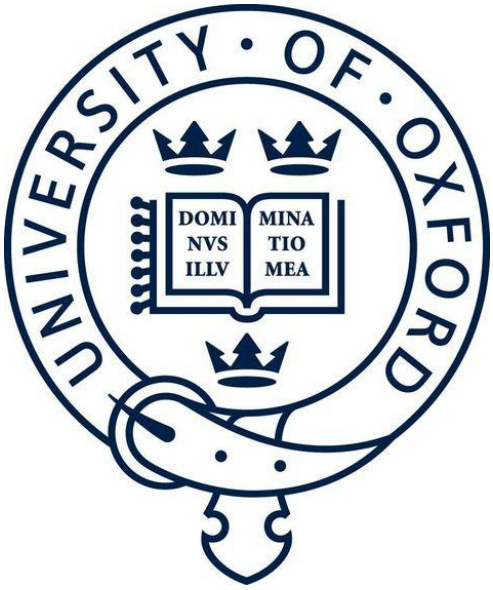
The influence of the social environment on strategic investment in competition



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For my family.

Abstract

Competitive behaviours are expected to emerge when the benefits of resource defence outweigh the costs. The costs and benefits of resource defence are in part modulated by the social environment, here defined as the composition of individuals of the same species within a population. Thus, changes to the social environment should be reflected through strategic modifications of individuals' investment into competition. Despite this expectation, we still lack empirical support or theoretical predictions that can fully elucidate how many aspects of the social environment influence competitive behaviour. In this thesis, I contribute to bridging this knowledge gap. First, I test how increasing competitor density alters individuals' propensity for, and distribution of, aggression across rivals in males of a cichlid fish, *Lamprologus ocellatus*. While previous studies (across species) often consider summed aggression across individuals, I show that aggression becomes confined to larger individuals in groups at higher competitor densities. Second, I seek to describe the individual and combined influences of sex ratio and environmental complexity (which alters individuals' perception of their social environment) on competitive behaviours in male red jungle fowl (*Gallus gallus*). I find no evidence for an interaction between sex ratio and environmental complexity but show support for their individual influences on intrasexual competitive behaviours. Third, I assess how the sex and age-composition of flocks influences female intrasexual aggression in red junglefowl. Further, I discuss the importance of sexual harassment (by males) and differences in sociality (within females) in mediating changes in aggression over time. Fourth, I develop a theoretical model to assess the influence of varying female reproductive quality on the size, stability and membership of coalitions where males cooperatively compete for access to reproductive opportunities. I demonstrate the importance of considering female reproductive quality – in combination with other facets of the social environment – for future empirical and theoretical studies of coalition formation. Overall, this thesis broadens our understanding of how competitive behaviours are shaped by the social environment, with applications for both animal welfare and predicting species' responses to a changing world.

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Chapter 1: *General Introduction*

When resources are limited, competitive interactions between individuals should emerge as a natural consequence (Darwin 1859, Darwin 1871). When competition occurs, the costs associated should lower the fitness of both individuals relative to the fitness obtained from not competing at all (Roughgarden 1979). Within species, competition can occur both between the sexes ('intersexual' competition) and within each sex ('intrasexual competition'). Because members of the same sex have similar resource requirements, intrasexual competition may more readily occur or be more intense than intersexual competition. Competition between individuals for resources can occur in two ways. First, when a resource is limited and accessible to all individuals (i.e. non-monopolisable), it may be shared equally across competitors ('scramble competition'). Second, when a resource is monopolisable by a single individual or group, the outcome may be despotic, and one party may be able to completely exclude others from the contested resource ('contest competition'), for example through fighting, endurance rivalries and ritualised displays (Nicholson 1954, Hardy and Briffa 2013).

Unlike in scramble competition, the outcomes of dyadic encounters in contest competition may be predictable, allowing individuals to strategically engage in contests depending on the probability of victory. In this thesis, I will explore the drivers of this strategic investment into competition.

1.1 Contest Competition Theory

Theory predicts that individuals should engage in contests whenever the benefits of contest competition (hereafter 'competition'), v, outweigh the associated costs, c (Maynard-Smith and Price 1973). In other words, competition should emerge as an evolutionary stable strategy (that is,

a strategy that is stable under natural selection) whenever $v/c > 1$. The benefit of competition can be defined as the improvement in survival and/or reproduction an individual receives as a result of obtaining (part of) a contested resource (Andersson 1994, Hardy and Briffa 2013), while costs of competition may encompass the potential for injury or death (Enquist and Leimar 1990), loss of time and energy available for other activities (Briffa and Sneddon 2007) and reputation costs (e.g. an individual losing rank within a group) (Tibbetts, Pardo-Sanchez *et al.* 2022). Overall, individuals will be more likely to engage in competition when v is high and/or c is low. However, when individuals vary in their competitive abilities, the decision to compete should be further influenced by the probability of obtaining v.

An individual's competitive ability, also known as its 'resource holding potential' ('RHP'), describes an individual's ability to obtain or retain a resource during competition (Parker 1974, Maynard-Smith and Parker 1976). Individuals of greater competitive ability are thus predicted to have relatively improved chances of survival or reproduction relative to conspecifics. The competitive ability of an individual may be predicted by morphological traits, such as body, testes, weapon or ornament, size (e.g. Maynard-Smith and Parker 1976, Møller 1990, Stockley, Gage *et al.* 1997, Bywater, Angilletta Jr *et al.* 2008), physiological states (e.g. Koskimäki, Rantala *et al.* 2004), or behavioural traits (e.g. boldness, Rudin and Briffa 2012). Individuals may use these traits to decide when to engage in, and withdraw from, contests by assessing the difference in RHP between themselves and competitors (Enquist and Leimar 1983). Alternatively, an individual may withdraw from a contest whenever the costs of competing exceed a threshold determined by their RHP, with no information obtained on the RHP of their rival (Mesterton-Gibbons, Marden *et al.* 1996, Payne and Pagel 1996).

When individuals can evaluate the RHP of others, contests should proceed in sequential stages of increasing intensity during which competitors gather information on their likelihood of success. At each stage of escalation, the performance of each contestant provides a more reliable estimate of the true difference in RHP between them, but this information comes at an increasingly higher price, as fight costs accumulate. An individual should withdraw from a contest whenever $pv < c$ (where p is the probability of winning), and contests between closely matched individuals are therefore predicted to endure for longer, reach a greater intensity, and incur higher costs (Enquist and Leimar 1983). This has been shown, for example, in the cichlid fish *Nannacara anomala* where contests escalate from visual displays to more costly aggressive interactions (intense tail beating), culminating in physical aggression (e.g. bites) if neither individual backs down (Enquist, Leimar *et al.* 1990). Further, complete avoidance or submission by one individual to another may occur when a large RHP asymmetry indicates to the weaker individual that $pv < c$ before any contest behaviour is initiated (Reddon, Ruberto *et al.* 2021).

1.2 Social Environment

The costs and benefits of competition are expected to be largely shaped by the social environment, that is, the composition of individuals within the population. Specifically, the frequency and intensity with which individuals partake in contest behaviour may depend on the density of rivals and the variation in their competitive abilities. By determining the distribution of competitive abilities in a population, the social environment can modulate the intensity and opportunity of selection on competitive traits (Darwin 1859). Alternatively, when competition occurs over mating opportunities, differences in the density and ability of competitors may alter the opportunity for, and intensity of, sexual selection (the selection arising from intrasexual competition over access

to reproductive partners; Darwin 1871, Emlen and Oring 1977). Additionally, the social environment may alter patterns of competition for reproductive partners when the benefits of competing for mates depends on variation in mate quality and the abundance of mates of the opposite sex (*vs* intrasexual competitors). Finally, individuals' perception of the population may be influenced by the complexity of their surrounding habitat, allowing for the social and physical environment to interact to modulate competitive behaviours.

1.2.1 Competitor density

When the value of a resource remains unchanged, the likelihood that an individual will engage in a contest should depend on factors that influence *c*, such as competitor density (Maynard-Smith and Price 1973, Grant 1993).

When the density of competitors is low, a contested resource may occur in greater abundance than the individuals competing for it. Consequently, individuals that don't engage in contests should acquire the same amount of a resource as those that do, but without incurring costs of competition (Grant, Gaboury *et al.* 2000, Grant, Girard *et al.* 2002). A 'peaceful' (no contest) strategy should thus pervade under a low competitor density if non-competitive individuals accrue a higher net *v* and ultimately gain greater fitness. As competitor density increases, the benefit of resource defence should begin to outweigh the costs, leading to contests arising more frequently. How contest behaviour is predicted to change with further increases in competitor density depends on the theoretical approach. According to optimality theory, once an 'upper threshold' of competitor density is reached, scramble competition should replace contest competition as a resource becomes uneconomical to defend (Brown 1964, Grant 1993). Alternatively, game theory predicts that contest competition should monotonically increase with competitor density, as individuals are

increasingly unlikely to encounter an uncontested resource (Maynard-Smith and Price 1973). These contrasting predictions can be reconciled by incorporating variation in competitive ability (and competitor roles; see Dubois, Giraldeau *et al.* 2003) into the game theoretic approach. Subsequently, the net benefits of contest competition are expected to peak at an intermediate competitor density according to both optimality and game theoretic approaches (see **Figure 1.1**).

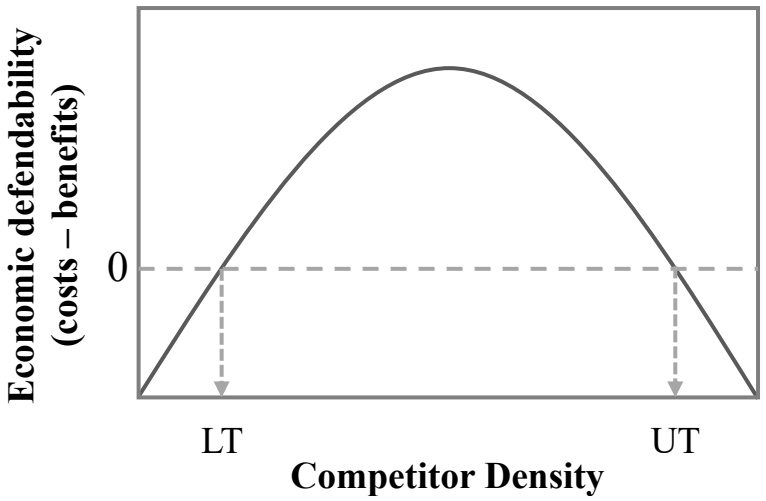


Figure 1.1: Contests should occur between lower (LT) and upper (UT) thresholds of competitor density (i.e. the area of the curve above the dashed line) and should peak at an intermediate competitor density. Adapted from Grant (1993).

Predicted peaks in the tendency of individuals to compete at an intermediate competitor density are supported by empirical data. For example, *per capita* rates of aggression in male Japanese rice fish (*Oryzias latipes*) were highest when either of two resources (food or mates) outnumbered competitors by a ratio of 2:1 (Grant, Gaboury *et al.* 2000, Goldberg, Grant *et al.* 2001). However, while the relationship between competitor density and contest frequency has been established, there is little understanding about how this affects underlying patterns of pair-wise interactions.

Specifically, it is unclear how individuals' propensity for, and distribution of, aggression varies with competitor density. In Chapter 2 of my thesis, I will explore this question (see 1.5 Thesis Aims).

1.2.2 Variation in competitive ability

Within a population, conspecifics are predicted to vary in their competitive abilities. The magnitude of this variation should be influenced by a number of factors, including genetic diversity (Hughes, Inouye *et al.* 2008), nutrient availability (Kvarnemo and Simmons 1999), and population size (Lande 1988). Such variation should influence the intensity of competition in a population when this leads to the outcome of contests becoming more or less predictable.

Altogether, populations with low variation in competitive ability may be expected to exhibit more intense competition because competitors are more often closely matched. Further, variation in competitive ability may influence with whom in a population an individual is most likely to compete. When there is low variation in competitive ability, individuals may compete with each other relatively indiscriminately owing to similarities in their RHP (Maynard-Smith and Parker 1976, Enquist and Leimar 1983). Conversely, when there is high variation in competitive ability, competition can be concentrated within sub-groups of individuals with similar RHPs, with contests occurring only occasionally between more dissimilar rivals. This latter prediction, termed the 'desperado effect', may occur when relatively weak (low RHP) individuals do not withdraw from any contests (including against rivals with a much higher RHP) due to a lack of alternative options for obtaining a resource (Grafen 1987). This effect may be more likely to occur when variation in competitive ability is high, as individuals with the lowest RHP may only encounter rivals with asymmetric, higher RHPs.

1.2.3 Variation in mate quality

When the value of a contested resource is higher, the condition that $v/c > 1$ should more often be met and competition should occur more frequently (Maynard-Smith and Price 1973). Further, an increase in v should result in individuals competing for longer, as it takes the eventual loser more time to establish that $pv < c$ (Enquist and Leimar 1983). While these statements are true for any type of resource, this concept is relevant to the social environment when competition determines access to other individuals (i.e. mates). The value of acquiring higher quality mates may include the production of more, or higher quality, offspring that ultimately increase an individual's genetic contributions to future generations (Clutton-Brock 1988).

When individuals with a greater RHP are more successful in competition over high quality mates, patterns of assortative mating may emerge (e.g. as seen in *Gammarus pulex*; Hume, Elwood *et al.* 2002). However, this scenario may be less likely when variation in mate quality is low. Indeed, when there is little difference in the quality of mates, any increase in v resulting from successful competition for a high-quality mate may be unlikely to outweigh the benefits of indiscriminate monopolisation (Edward and Chapman 2011). Overall, strategic investment into competition over mates may become more apparent when there is high variance in mate quality.

1.2.4 Operational Sex Ratio

Across species, the intensity of competition for mates can be estimated by the 'operational sex ratio' (OSR), that is, the ratio of sexually receptive males to sexually receptive females in a population (Emlen and Oring 1977). The tendency of either males or females to skew the OSR should depend on sex-specific differences that govern their potential for polygamy (the ability of

an individual to mate with multiple partners in the same reproductive cycle; see 1.4 Sex Roles). While changes in OSR can occur due to changes in competitor density (as described in 1.2.1 Competitor Density), this can also be driven by changes in the density of resources (mates) against a constant number of competitors. In both of these cases though, the economic defendability of mates should follow a dome-shaped curve as the competing sex moves from being under- to over-represented in the population (Emlen and Oring 1977, Grant 1993).

The economic defendability of mates is expected to peak when the OSR is moderately skewed towards a focal sex (e.g. as seen in Japanese rice fish, *Oryzias latipes*; Grant, Gaboury *et al.* 2000). Under these conditions, monopolisation of mates by one, or few, individuals should result in a large variance in reproductive success across the focal (over-represented) sex. High rewards (v) of monopolising access to mating opportunities should promote intense intrasexual competition between members of the over-represented sex (Maynard-Smith and Price 1973). In addition, intense competition may result in an increased frequency of intersexual interactions when female choice remains an important predictor of reproductive success (Weir, Grant *et al.* 2011). For example, in Japanese rice fish, the courtship rate of both males and females increases as the OSR becomes biased towards either sex, respectively (Clark and Grant 2010).

1.2.5 Environmental Complexity

The influence of the social environment on modulating competition may depend on the complexity of the physical environment (Emlen and Oring 1977). For example, in three-spined sticklebacks (*Gasterosteus aculeateus*), structural complexity within an environment (e.g. dense vegetation) may reduce encounter rates between conspecifics, leading to less frequent contests despite no changes to the net benefit of competing (Patullo, Baird *et al.* 2009). Reduced encounter rate, as

introduced by environmental complexity, may additionally lead to individuals erroneously responding to their social environment (see Candolin, Salesto *et al.* (2007) for discussion of similar effects in the context of mate choice). Specifically, if the standard error of an estimate is inversely related to sample size, low encounter rates may lead to overestimates of variance in competitive ability and/or mate quality, thereby altering individuals' propensities to compete. Finally, environmental complexity may lead to sex-specific changes in spatial distribution that alter the net benefits of competition. In elephant seals (*Mirounga* spp.), the suitability of beaches dictates the spatial clumping of females (i.e. resource density) and the associated costs and benefits to males of resource defence (Brown 1964, Boness 1991). In killifish (*Nothobranchius* spp.), males retreat to vegetated areas to avoid predation, resulting in local variations in the OSR (Reichard, Polačik *et al.* 2014). Despite clear predictions that environmental complexity should influence the social environment, there is little understanding of how these factors interact to modulate patterns of competition. In Chapter 3 of my thesis, I will contribute to closing this knowledge gap by investigating the combined effects of environmental complexity and sex ratio on intrasexual competitive behaviours (see 1.5 Thesis Aims).

1.3 Social Organisation

When aspects of the social environment vary, patterns of social organisation may emerge, which reduce the costs associated with contest competition. For example, this may arise when high quality resources attract more competitive individuals that can better limit the competitive success of inferior rivals. As a result, less competitive individuals may seek out resources of lower quality that are relatively uncontested, leading to heterogeneity in the distribution of individuals with particular ranges of RHP in the social environment (Parker and Sutherland 1986). Alternatively,

individuals may gather information about conspecifics and adjust their behaviour strategically in response to that information (Ward and Webster 2016). Two examples of such social organisation that I expand upon in my thesis are dominance hierarchies and coalitions.

1.3.1 Dominance Hierarchies

Dominance relationships are established when the outcome of competition determines 'winners' and 'losers' of contests (Tibbetts, Pardo-Sanchez *et al.* 2022). When continued conflict occurs within small groups of familiar individuals, dominance relationships may be formalised into dominance hierarchies where differences in RHP give rise to social ranks. These ranks dictate priority of access to contested resources (e.g. food or mates), without the need for recurring contests (Kaufmann 1983). Once established, social hierarchies may be enforced through dominance signalling, and avoidance of dominant individuals by subordinates (Clutton-Brock and Parker 1995). However, when reversal of social ranks *via* contest competition is possible, subordinates may challenge dominant individuals in order to improve their social status (Dehnen, Papageorgiou *et al.* 2022).

Overall, the occurrence of aggression within dominance hierarchies should depend on how the composition of individuals modulates opportunities for enforcing and challenging social ranks. For example, previous work indicates that in some socially structured populations, dominant individuals may influence aggression among subordinate individuals. However, the mechanisms underpinning these behaviours and their functional significance remain unclear. In Chapter 4, I will seek to resolve these patterns (see 1.5 Thesis Aims).

1.3.2 Coalitions

Despite the expectation that resource limitation should encourage selfish competition among rivals, coalitions may also arise as a paradoxical form of social organisation (Díaz-Muñoz, DuVal *et al.* 2014). Cooperative coalitions occur when two or more individuals forego competition with each other and instead jointly direct competitive behaviours towards their rivals (Taborsky 2009). Such displays of cooperation are mostly reported for males in various mammalian taxa, including bottlenose dolphins (*Tursiops aduncus*) and baboons (*Papio cynocephalus*) who form intrasexual coalitions in order to improve access to reproductive opportunities (Noë 1990, Connor, Heithaus *et al.* 2001, Connor and Krützen 2015; but see Díaz-Muñoz, DuVal *et al.* (2014) for similar behaviours in other taxa). Further, males from many macaque species (including *Macaca assamensis* and *M. nigra*) form competitive coalitions in order to ascend or defend positions within dominance hierarchies (Schülke, Bhagavatula *et al.* 2010, Neumann, Kulik *et al.* 2022). Although cooperative coalitions often necessitate the sharing of rewards (e.g. mating opportunities; reviewed in Díaz-Muñoz, DuVal *et al.* 2014), the benefits they confer should both outweigh the associated costs and the net benefits of competing alone. For example, male dolphins that form cooperative coalitions enjoy a substantial increase in reproductive success compared to those that do not (Krützen, Barré *et al.* 2004). In some extreme cases, coalition rewards may be completely skewed towards one individual, so that other partners receive nothing (e.g. in Colombian red howlers, *Alouatta seniculus*). In these instances, individuals bereft of rewards may still benefit, for example, if coalition partners are relatives (Pope 1990).

As with other competitive behaviours, the costs and benefits of coalition formation are expected to be modulated by the social environment (Whitehead and Connor 2005). Given that coalitions

are typically formed in response to intrasexual competition over access to mates, an aspect of the social environment of fundamental relevance to coalition formation is variance in mate quality. To date however, the influence of varying mate quality on the tendency of males to form coalitions remains little studied. In Chapter 5 of my thesis, I will address this using a theoretical model, allowing for a more complete understanding of the effect of the social environment on coalition formation (see 1.5 Thesis Aims).

1.4 Sex Roles

While both sexes should compete for resources necessary for survival, males and females typically show pronounced differences in their tendencies to compete for mating opportunities (Clutton-Brock and Vincent 1991). These differences are widely attributed to higher reproductive costs of gamete production and maternal care, which constrain females' potential reproductive rates relative to males (Parker, Baker *et al.* 1972, Trivers 1972). Male potential reproductive rates are therefore limited by the availability of sexually receptive females, typically resulting in a male biased OSR that promotes competition between males to obtain and defend access to mates (Bateman 1948, Emlen and Oring 1977). Indeed, examples of male competition for mates are prevalent across the animal kingdom (e.g. mate guarding by male baboons, *Papio cynocephalus*, to reduce or prevent post-copulatory sperm competition, (Alberts, Altmann *et al.* 1996); the formation of leks by male black grouse, *Tetrao tetrix*, where males competitively display to females, (Alatalo, Höglund *et al.* 1991); or aggressive resource defence by male fruit flies, *Drosophila melanogaster*, to attract prospective mates, (Baxter, Barnett *et al.* 2015); see also (Janicke, Häderer *et al.* 2016) for a meta-analysis on sex roles). While low reproductive costs should result in males mating indiscriminately with any available female, females should act to

offset their relatively high reproductive investment by discriminating (i.e. being 'choosy') among mating opportunities (Darwin 1871). Resultingly, patterns of female mate choice should reflect direct (improved fecundity or survival) or indirect (improved offspring viability or attractiveness) benefits of preferentially mating with a subset of available males (Wong and Candolin 2005).

Despite these traditional views of sex roles, there is accumulating evidence to suggest that both mate competition and mate choice are behaviours that are broadly present in both males and females (Clutton-Brock and Huchard 2013). While the potential reproductive rate of females is less often limited by the availability of mates, females may compete for other resources necessary for reproduction, such as food or nesting sites (Campbell 2004, Stockley and Bro-Jørgensen 2011). For example, female hyenas (*Crocuta crocuta*) compete for social dominance to obtain better access to food and other resources required for improved reproductive performance (Holekamp, Smale *et al.* 1996). Moreover, female wood ducks (*Aix sponsa*) aggressively compete for access to nesting cavities required to lay their eggs (Semel and Sherman 2001). While competition may represent an additional cost of reproduction, females are expected to pursue contests when these collective costs are outweighed by the benefits of improved reproductive success.

Similarly to females, males can incur substantial costs of reproduction, including competing for mates (mate guarding, lekking and aggressive defence described above), ejaculate production (Dewsbury 1982) and paternal care (e.g. Wright 1990, Goldberg, Downing *et al.* 2020). When these costs exceed the value of mating with all available females, males should become more selective over reproductive opportunities, including showing restraint over when to compete, and who to compete with, for mates.

Overall, both males and females are expected to compete over resources necessary for reproduction, such as mates, food, and nesting sites. However, the value of accessing these resources should be measured against combined costs of competition and reproduction, leading to strategic engagement in competition. In this thesis I will investigate aspects of strategic competition that occur separately for both males and females.

1.5 Thesis Aims

In this thesis, I will investigate how strategic investment in competition is influenced by aspects of the social environment.

In **Chapter 2**, I examine how changes in competitor density regulate networks of competitive interactions between individuals. To do this, I conduct observations using males of the cichlid fish *Lamprologus ocellatus* as aggression in Cichlidae spp. is broadly reported to be modulated by competitor density. I show that aggression increases with competitor density, though this change appears to be driven by increasing instances of aggression among larger individuals.

In both **Chapter 3** and **Chapter 4**, I use the red junglefowl (*Gallus gallus*) to determine how aspects of the social environment regulate competitive behaviours. In **Chapter 3**, I investigate how adult sex ratio and environmental complexity modulate patterns of male competitive behaviours. I show that males respond to changes in sex ratio by altering aggressive behaviours and daily patterns of dominance signalling.

In **Chapter 4**, I supplement flocks of young females with a male, an old female, or an additional young female to understand how the composition of a group modulates temporal patterns of female intrasexual aggression. I show that initial patterns of intrasexual aggression – and temporal trends

thereafter – are influenced by both the sex- and age-composition of individuals within the social environment.

In **Chapter 5**, I use a theoretical model to explore how variation in female reproductive quality interacts with additional aspects of the social environment to modulate the tendency of males to form coalitions. Using model outputs, I demonstrate that increased variance in reproductive quality is predicted to lead to larger, more unstable coalitions forming between males. Additionally, I parameterise my model with previously collected species data and show this models' predictions on coalition formation are partially accurate when compared to observed trends.

Chapter 2: *The influence of stocking density on patterns of aggression in the cichlid fish*, Lamprologus ocellatus

Hannah Ogden, Emily Scott, Josh Firth, Tommaso Pizzari, Eleanor Bath, & Jonathan Green

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Author contributions: Jonathan Green and I conceived of and designed the study. Emily Scott and I collected the data. I discussed the methods of data analysis with Josh Firth. I analysed the data and wrote the manuscript. The chapter was edited to incorporate comments from Tommaso Pizzari, Jonathan Green and Eleanor Bath.

2.1 Abstract

With increasing competitor density, instances of competitive behaviours, including aggression averaged *per capita,* are theorised to initially increase, then subsequently decline as the costs of competition exceed the benefits. Evidence of this concave response to competitor density has been reported in numerous species and is often used to inform husbandry practices. However, there is currently little information on interindividual variation in responses to changing competitor density and how this drives group-level changes in cumulative aggression. In this study, we investigated patterns of aggressive behaviour across competitor (stocking) densities in male *Lamprologus ocellatus*; a commercially traded fish species in which aggression among males is common and detrimental to welfare. First, we showed that cumulative counts of aggression increased across stocking densities, rather than showing a concave relationship as predicted by theory and

husbandry practices. Second, we explored changes in individuals' propensity for, and distribution of, aggression across stocking densities. We found that with increasing stocking densities (a) larger males initiated more aggression; (b) variation in aggression initiated and received among individuals increased; and (c) aggression increased between opponents more similar in body size. These results indicate that aggression among male *L. ocellatus* becomes increasingly restricted to larger individuals at high competitor densities. In addition to our experimental aims, we surveyed fishkeepers on husbandry practices and found that 70% of respondents stocked fish at high densities to reduce aggression. We suggest that the benefits of stocking fish at high densities are not from reduced aggression *per se*, but from larger fish being better able to endure the costs of fighting, leading to less severe outcomes of aggression across group members. Future studies may consider how changes to competitor density can be combined with additional factors, such as environmental complexity, to incite further reductions in aggression for *L. ocellatus*, and other, species.

2.2 Introduction

Animal contests, including aggressive resource defence, are expected to arise and proceed so long as the expected benefits of competitive success to an individual exceed the costs (Maynard-Smith and Price 1973). Costs and benefits of competition may vary even when the quantity and quality of a resource remains the same. For example, when there is a low density of competitors, access to a resource may be achieved without costly defence, meaning aggression is less likely to occur (Grant 1993). With increasing competitor density, reduced access to resources should increase the benefits of defence, leading to contests arising more frequently. However, as competitor density increases beyond a certain point, contest behaviour is expected to decline as resources become uneconomical to defend and individuals resort to scramble competition. Overall, this leads to the theoretical prediction that averaged *per capita* aggression within a group (hereafter 'group-level aggression') should follow a dome-shaped (hereafter 'concave') function of group size (Grant 1993, Dubois, Giraldeau *et al.* 2003). This concave relationship has been demonstrated in a number of species, including Japanese rice fish (*Oryzias latipes*) where aggression among males peaks at an intermediate competitor-to-resource ratio (Grant, Gaboury *et al.* 2000; see also Goldberg, Grant *et al.* 2001, Grant, Girard *et al.* 2002, Caballero and Castro-Hdez 2003 for examples across taxa). Further, the expectation of a concave relationship between aggression and density is often used to inform husbandry practices, for example in pigs (*Sus scrofa,* Andersen, Nævdal *et al.* 2004), chickens (*Gallus g. domesticus,* Estevez, Newberry *et al.* 2002) and ornamental fish[1,2], where housing individuals (competitors) at low densities may not be economically viable.

[1] https://www.ratemyfishtank.com/blog/african-cichlid-aggression-how-to-reduce-aggression
[2] https://www.practicalfishkeeping.co.uk/features/the-mbuna-keepers-survival-guide/

Evidence for a concave relationship between aggression and stocking density usually describes changes to cumulative counts of aggression that are averaged across individuals (Grant, Gaboury *et al.* 2000, Goldberg, Grant *et al.* 2001, Grant, Girard *et al.* 2002, Caballero and Castro-Hdez 2003). It is less understood, however, whether these changes are driven by uniform responses of individuals to increases in competitor density. Within a population, individuals are expected to vary in their propensity for aggression and in which (and how many) rivals they direct their aggression towards. One source of inter-individual variation in aggression is resource holding potential (RHP), that is, the ability of an individual to succeed in a fight (Parker 1974). As competitor density increases from low levels and resources become economical to defend, individuals may benefit from pursuing contests. Moreover, individuals may preferentially pursue contests with opponents against whom they have some chance of success, such as those with a similar or lower RHP (Enquist and Leimar 1983).

With further increases in competitor density, the net benefits of resource defence should lessen as excluding each rival will have a smaller effect on shrinking the pool of competitors. At higher stocking densities, declining propensities for aggression and more potential rivals should result in individuals distributing aggression towards proportionally fewer opponents. Based on this expectation, two additional predictions can be made. First, individuals at high competitor densities may preferentially direct aggression towards weaker rivals ('bullying' *sensu*; Hobson, Monster *et al.* 2021) against whom the energetic costs of contest success are lower. However, the benefits of excluding these rivals may be limited, assuming that individuals consume resources proportionally to their RHP (Parker and Sutherland 1986). Thus instead, individuals may preferentially direct aggression to exclude evenly matched rivals, incurring a higher cost of competition but receiving proportionally more benefits (e.g. if rewards are split among remaining competitors according to

RHP). These predictions represent alternative strategies by which individuals maximise net benefits of competition, with strategies conceivably depending on the competitive environment (Hobson, Monster *et al.* 2021). In addition to changing distributions of aggression, individuals may vary in their propensity for aggression across stocking densities (Grant 1993). For example, if certain individuals (such as those with a greater RHP) incur lower costs of competition, individuals may show greater variation in the amount of aggression they initiate as competitor density increases (e.g. suggested for *G. g. domesticus*, Estevez, Keeling *et al.* 2003) (Briffa and Sneddon 2007). This may be particularly problematic with regards to welfare, for example if persistent aggression from few individuals at high competitor densities is consistently targeted towards particular rivals. Overall, elucidating patterns of individual-level aggression has applied importance, as well as general importance for understanding how selection pressures of competition are shaped by the competitive environment.

Cichlid fish are a particularly useful family in which to study aggression. This is due to the prevalence of paternal care which encourages aggressive territorial behaviour by males (Ah-King, Kvarnemo *et al.* 2005). Across fish, differences in body size are a major predictor of RHP, with larger individuals generally achieving greater success in competition (Earley and Hsu 2013). The Cichlidae family is notably large and diverse, containing many species that are kept and sold as part of the ornamental fish trade (Takahashi and Koblmüller 2011). Intraspecific aggression is frequent in cichlids, with negative economic and welfare impacts when involvement in contests reduce individual health and survival (Oldfield 2011, Brandão, Dorigão-Guimarães *et al.* 2021, Jones, Alexander *et al.* 2022). Within the ornamental fish trade, aggression among cichlids is managed to an extent by removing contestable resources (e.g. substrates used for spawning; Taborsky 2016) but, it cannot be fully prevented as individuals still seek to establish territories

when grouped together in small tanks. Stocking tanks at high densities is a further measure to reduce persisting aggression, though, to our knowledge, this has only been anecdotally described and scientific research into the effectiveness of this approach is lacking. In particular, studies are needed to determine whether aggression declines at high competitor densities (as predicted by resource defence theory) and to examine the changes in individuals' propensity for, and distribution of, aggression that underlie this response.

Here, we investigated how stocking (competitor) density influences patterns of aggression in males of the shell-dwelling cichlid, *Lamprologus ocellatus* (Family: Cichlidae). In their natural habitat of Lake Tanganyika, males defend territories with multiple empty gastropod shells (of the genus *Neothauma*) within which one or more females will settle and use the shells to spawn and care for offspring (Bills 1996). *L. ocellatus* are a popular species within the ornamental fish trade and aggression among males, as with other cichlid species, is problematic.

In this study, we tested whether group-level aggression showed a concave response to increasing competitor density, as predicted by resource defence theory. Next, we sought to describe how group-level changes in aggression across stocking densities manifested at the individual-level. To test this, we first measured how the propensity for individuals to be aggressive varied with stocking density. We predicted that individuals would initiate less aggression as competitor density increased, but that individuals with a higher RHP would be slower to reduce their aggression. As such, we expected this to increase the variance of aggression initiated by individuals at higher competitor densities. Second, we measured variation in aggression received by individuals to understand how the distribution of aggression within a group varied across stocking densities. In addition, we tested whether the distribution of aggression was related to body size (a proxy of RHP), and whether these patterns varied with stocking density such that aggression becomes

preferentially focused on particular rivals (e.g. either smaller and weaker, or evenly matched individuals). Finally, we distributed a survey to ornamental fish traders to understand how frequently stocking at high densities is used as a tool to manage aggression.

2.3 Methods

2.3.1 Experimental Animals and Housing

Individuals used in this study were selected from ten captive-bred lines (A-B and E-L) housed at the University of Oxford's John Krebs Field Station. All individuals were sexually mature, though their precise age was not known. For the duration of the study (April – October 2022), individuals were housed in 40L tanks (60 x 30 x 30cm) with a sand substrate (5cm depth). Water temperature was maintained at 26 ± 1°C, pH at 8.4, gH at 22-26 and kH at 8-11. Fish were fed twice daily with Tropical Tanganyika Flakes®, except for one afternoon a week when they received brine shrimp. No shells were supplied to any tanks to avoid intense territorial aggression and breeding. Outside of observations, fish were housed singly or in mixed-sex groups of 2-13 individuals. For observations, males were assembled into groups of different sizes (see below).

2.3.2 Group Assembly

In our study, we considered 4 stocking densities of: 4, 6, 8 or 10 males *per* tank, with 7 replicates of each stocking density. Within fishkeeping, there is a marked lack of universal or species-specific guidelines advising suitable ranges of stocking densities (Home Office 2014, Stevens, Croft *et al.* 2017). For this study, we selected 10 males *per* tank as the highest stocking density due to difficulties with measuring behavioural interactions between more individuals than this.

Due to constraints on the number of males available for the study, individuals were reused across groups. Each group, however, contained a unique composition of individuals, such that individuals from one group were never found all together in another group of the same, or larger, size. Again, due to constraints on available males, many groups contained multiple males from the same line. There is currently little understanding of the genetic basis for variation in aggression, though it is possible that the composition of fish from across different lines influenced aggression among groups. However, the heritability of aggression is low and unlikely to exceed body size (accounted for in this study) as a predictor of competitive success across groups (Earley and Hsu 2013). Further, although males from separate lines were assumed to be unrelated, the relatedness of males within lines was unknown and males may have ranged from unrelated to full siblings. As, there is no evidence for kin recognition among *L. ocellatus*, potential variance in the relatedness of groups was assumed not to affect the distribution of aggression therein.

While individual recognition has not been established in *L. ocellatus* (though see Hert (1985) and Balshine-Earn and Lotem (1998) for examples in related Lamprologine spp.), individuals were left for at least six days once groups were assembled as it was assumed some level of familiarity may be required to stabilise interactions (also see other taxa where this is the case: Höjesjö, Johnsson *et al.* 1998, Foris, Haas *et al.* 2021). Occasionally, group formation caused short-term stress in certain individuals (detectable through a change in body coloration). When this occurred, small barriers were placed into tanks to provide refuges for a duration of less than six days. As fish continued to swim around the tank in the presence of these barriers, it was assumed that they did not restrict interactions with other group members. When one or more fish appeared to be stressed for many days, groups were re-assembled (swapping out stressed fish) and left for another 6 days before observations.

2.3.3 Data Collection

Filming

To investigate how patterns of aggression changed across stocking densities, groups were filmed using GoPro HERO8 and HERO7 cameras. Aggression in this population typically peaks during and immediately after feeding (J. P. G., personal communication). Because these periods of heightened aggression may obscure more subtle effects of stocking density on aggression, filming took place at least 1 hour after the morning feed. To ensure all interactions could be reliably observed, two cameras (providing two viewing angles) were used to film each group. All videos were taken at 1080p resolution and 120 frames per second.

Fish were filmed for a 30-minute observation period following the departure of the observer (H. J. P. O. and E. S.) from the room. Following the observation period, the body size of fish was measured by gently restraining each individual in a net against the front of the tank and using a digital calliper to measure the distance between the tip of the snout and the caudal peduncle (to the nearest 0.1mm).

Data Extraction

In common with other cichlid species, *L. ocellatus* display a number of aggressive behaviours, including chasing and mouth wrestling (Frostman and Sherman 2004, Hick, Reddon *et al.* 2014, O'Connor, Reddon *et al.* 2015). In this study, instances of chasing were used to quantify aggression, since initiators and recipients of this behaviour could be reliably identified. Chasing was recorded when one individual (aggressor) swam towards another individual (recipient) holding their pectoral fins erect, coming within one body length of the recipient or pursuing them

in cases where the recipient moved away. Instances of chasing between the same two individuals were considered distinct when chasing bouts were separated by at least three seconds of no chasing. Chasing was ignored when the aggressor was itself being chased by a third-party, as in such cases it was unclear whether one or two individuals were initiating aggression. Chasing was further classified as successful when the recipient moved at least one body length away from the aggressor or rotated their body by at least 90° from the aggressor. Chases were considered unsuccessful when this did not occur. Aggression was classified this way as the directionality of an unsuccessful chase (where the recipient refuses to respond) may be less clear than that of a successful chase, with different implications for the balance of RHP within a dyad.

Chases were recorded from video observations of each replicate group. To quantify the amount of aggression given and received by each individual in a group, videos were watched *n* times (where *n* is the group size) with continuous observation of a different focal individual each time. Focal individuals were individually identified by their position within the tank at the beginning of recordings. The video timestamp and whether individuals were the initiator or receiver of aggression was recorded for each successful and unsuccessful chase. Once the behaviour of each fish had been recorded, dyads involved in each aggressive interaction were established by matching fish who initiated and received aggression at the same time. Overall, this allowed weighted, directed networks of aggression between individuals to be recorded *per* group within each stocking density.

A Spearman's rank correlation test indicated no significant association between summed counts of successful and unsuccessful chases occurring within each replicate group (Spearman's *rho* = 0.316, $p = 0.102$; total successful chases across groups = 4613; total unsuccessful chases across groups = 193). Counts of unsuccessful chases were low (mean 6.893 ± 1.166 SE *per* group),

limiting the statistical power for understanding how this behaviour varied across stocking densities. As such, only counts of successful chases were used as a measure of aggression in this study.

2.3.4 Statistical Analysis

Statistical analyses were conducted in R (v 4.1.1) (R Core Team 2013). Unless otherwise stated, linear models described below were run using the 'lme4' package (Bates 2010) and analysed using a Wald *F*-test (type III for models with significant interactions and type II otherwise). Post-hoc analyses were run using the 'emmeans' package (Lenth, Singmann *et al.* 2019).

Group-level Aggression

To test how group-levels of aggression varied across stocking densities, counts of chasing were summed within groups and divided by the number of individuals in the group. Group-level aggression was entered as a response variable in a linear model with stocking density as a fixed effect. A quadratic term for competitor density was initially included in the model to test whether aggression followed a concave relationship previously established for other systems (Grant, Gaboury *et al.* 2000, Goldberg, Grant *et al.* 2001, Grant, Girard *et al.* 2002). However, as the addition of this quadratic term did not significantly improve the model fit (tested for using the *anova* function in the 'stats' package), this term was not included in the final model. Normality of model residuals was confirmed using the *check_normality* function in the 'performance' package (Lüdecke, Ben-Shachar *et al.* 2021).

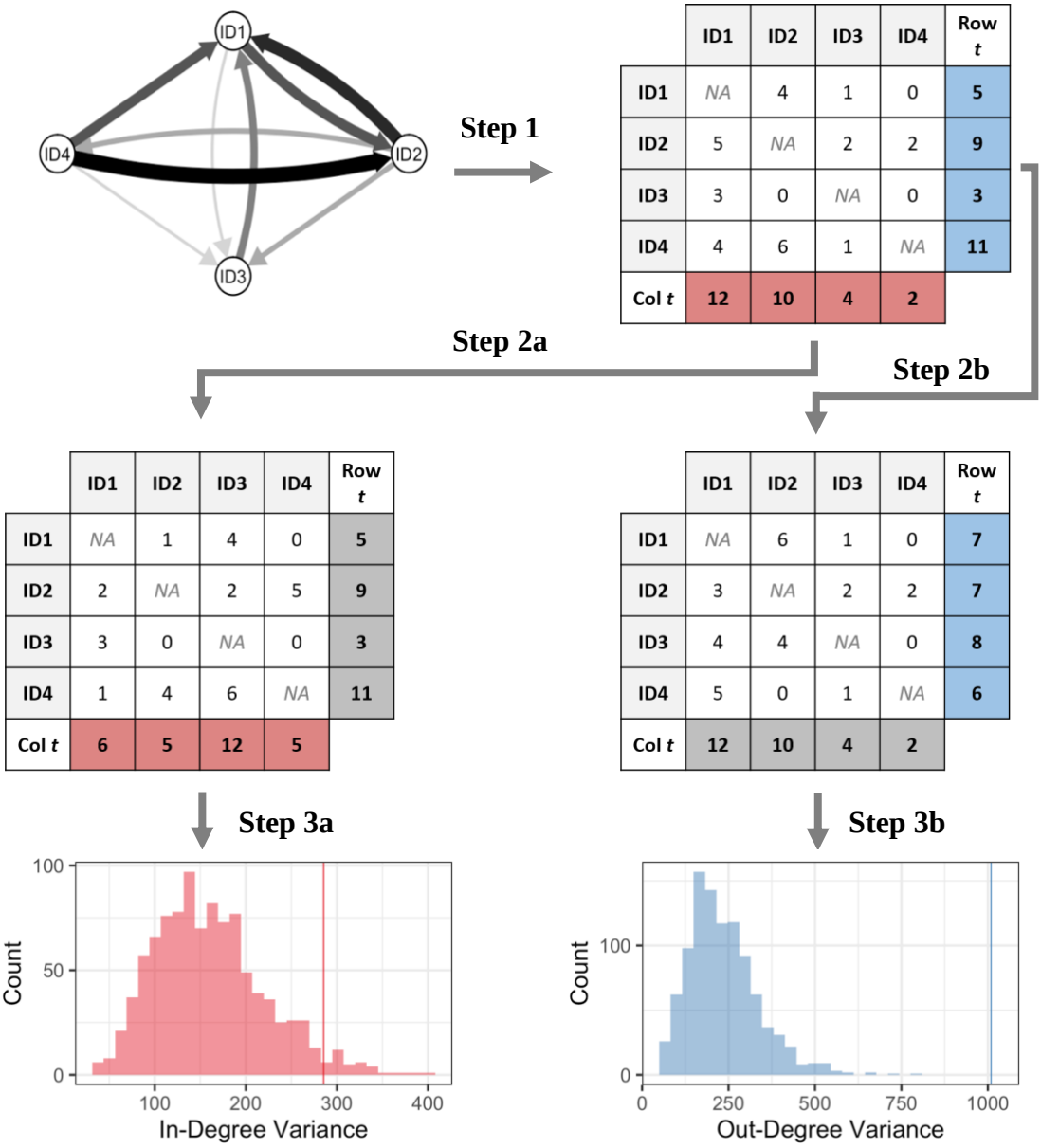
Network Analysis

To test whether stocking density influenced individuals' propensity for aggression and how this aggression was distributed across rivals, we generated networks of aggressive behaviour (chasing) for each replicate group. Within networks, each individual was represented by a node. Network edges showed the direction of aggression (initiator to target) and were weighted by the total count of aggression for each dyad.

For each replicate group, we calculated the extent to which individuals varied in how much aggression they received and, separately, how much aggression they initiated. In other words, we calculated the variance of the summed edges directed into, and out of, each node (degree variance test statistics, termed 'in-degree' and 'out-degree' respectively; see **Figure 2.1**). Measures of variance for in- and out-degrees should be 0 when all individuals receive or initiate the same amount of aggression as each other and should increase from 0 the more these values of aggression differ.

Direct comparisons of degree variance across stocking densities may be problematic if increased group size leads to a greater scope for variance in social network structure. In other words, observed differences in degree variance across stocking densities may simply be a consequence of increasing the number of nodes within a social network rather than changes in patterns of behaviours *per se*. To account for this influence of network structure, we used permutations to create a null distribution and compared degree variance from these to those of our observed networks. Differences in measures of null and observed test statistics thus imply that variation in individuals' propensity for, and distribution of, aggression that cannot only be explained by network structural properties (i.e. node number).

Network permutations were created for each replicate group by redistributing aggression across individuals, keeping constant the edge number and edge weight given (in-degree) or received (out-degree) *per* individual (see **Figure 2.1**). 1,000 network permutations were used to generate null distributions of variance for each degree type. Observed variance in in- and out-degrees for each replicate group were compared to their respective null distributions. Observed test statistics that fell outside the 95% range of values predicted under the null distribution were considered to be significant (equivalent to $p < 0.05$ level in a two-tailed test). In other words, significant deviations in the variance of in- and out-degree from null distributions indicated that there was non-random variation in the propensity of individuals to receive and initiate aggression, respectively.



	ID1	ID2	ID3	ID4	Row *t*
ID1	*NA*	4	1	0	5
ID2	5	*NA*	2	2	9
ID3	3	0	*NA*	0	3
ID4	4	6	1	*NA*	11
Col *t*	12	10	4	2	

	ID1	ID2	ID3	ID4	Row *t*
ID1	*NA*	1	4	0	5
ID2	2	*NA*	2	5	9
ID3	3	0	*NA*	0	3
ID4	1	4	6	*NA*	11
Col *t*	6	5	12	5	

	ID1	ID2	ID3	ID4	Row *t*
ID1	*NA*	6	1	0	7
ID2	3	*NA*	2	2	7
ID3	4	4	*NA*	0	8
ID4	5	0	1	*NA*	6
Col *t*	12	10	4	2	

Figure 2.1: Schematic representation of the two permutation methods. For each replicate group, weighted, directed networks were re-visualised as matrices, where rows indicated aggression received *per* individual and columns indicated aggression initiated *per* individual (**Step 1**). In **Step 2a**, edge weights were randomly redistributed across matrix rows, leading to changes in the column totals (aggression received *per* individual). Calculating the variance across column totals of this permuted network provides a null measure of variance in in-degree. Alternatively, in **Step 2b,** edge weights were randomly distributed across matrix

columns allowing a null measure of variance in out-degree to be calculated. **Steps 2a** and **2b** were each repeated 1,000 times to create null distributions of variance in degree types to which test statistics (solid coloured lines) of variance in in- and out-degrees could be compared (**Steps 3a** and **3b**).

The Role of Body Size

Initiation of aggression

To test whether individuals' propensity to initiate aggression varied with body size across stocking densities, we ran a model with counts of aggression initiated by each individual as the response variable. Body size (mm) was entered into the model as a covariate alongside a fixed effect of stocking density. As fish were assumed to respond to relative differences in body size among immediate rivals, body size was standardised within replicate groups using the *scale* function. To test whether the relationship between body size and individual aggressiveness varied with stocking density, we included an interaction term for these effects. To control for within-group variation in aggression, replicate group was entered into the model as a random effect. As counts of initiated aggression were right-skewed, we initially fitted the model with a Poisson distribution. However, this led to significant overdispersion of the model ($\chi^2 = 4043.291$, $p < 0.001$). The model was thus re-run with a negative binomial distribution using the 'glmmTMB' package (Brooks, Kristensen *et al.* 2017).

Aggression within dyads

To test if differences in body length between competitors predicted aggression, and whether this varied across stocking densities, we ran two models. As the differentials in body size among

individuals should decrease with increasing group size, the body lengths of all individuals were standardised within groups using the *scale* function.

In the first (proportional) model, the proportion of chases initiated by the larger individual within each dyad was entered as the response variable into a generalised linear mixed model. Here, only dyads where at least 1 chase had been initiated by either individual were included. The model was weighted by the total number of chases *per* dyad such that more emphasis was placed on proportional values from dyads where more aggression had occurred. In the second (binary) model, we considered all possible dyads of individuals within groups. This allowed us to incorporate dyads in which no aggression occurred. For each dyad, we assigned a binary aggression score (1 = at least one chase initiated by either individual in the dyad and targeted towards the other; 0 = no aggression within the dyad). These scores were entered as the response variable into a generalised linear mixed model.

Within each group, all individuals were assigned a unique ID and these IDs were distinct across groups. To account for repeated observations of aggression initiated or received by each individual (*albeit* within different dyads), unique IDs of the larger and smaller individual within each dyad were included as separate random effects for both (binary and proportional) models. In the binary model, both unique ID random effects explained very little variance ($<10^{-18}$) in the response variable and were removed from the model to avoid singularity effects. Instead, a random effect of replicate group was included to account for intra-group variation in aggression. Both models were fit with a logit-link binomial-error distribution.

Power Analyses

For statistical tests examining the role of body size, the sample size for each replicate group was determined by the stocking density. For example, each replicate group in stocking densities of 4 and 10 were represented by 4 and 10 data points when individual aggression was considered, and 6 and 45 data points when dyadic aggression was considered. As such, the statistical power to detect significant patterns may have been lower in smaller stocking densities. To account for this, power analyses were conducted when post-hoc tests of statistical models revealed that significant results were restricted to larger stocking densities. These analyses tested whether our sample size lent sufficient power (>80%) to the statistical model to detect a significant effect within smaller stocking densities. Instances where power analyses were used are highlighted in the Results. Power analyses were run using the *powerSim* function in the 'simr' package (Green and MacLeod 2016). The effect size (i.e. the assumed statistical value required to achieve a significant result) for each power analysis was determined retrospectively based on the model output and is reported in the Results.

2.3.5 Survey

To understand how regularly aggression among cichlids species is managed by stocking fish at high densities, we distributed a survey to ornamental fish traders via email (see Appendix A for a more detailed description of the survey). In addition to surveying the frequency with which respondents use high stocking densities, we also asked respondents to describe any other methods they used to manage aggression. Further, to respondents that indicated they used overstocking to manage aggression, we asked for anecdotal descriptions on the effectiveness of this method.

The survey was built using the JISC survey tool (https://www.onlinesurveys.ac.uk/). Email addresses of participants were identified from websites returned by the Google search term: "aquarist" OR "aquarium shop" AND "cichlid" AND "UK". In total, the survey was distributed to 57 traders in the UK, resulting in 10 replies.

2.3.6 Ethics Statement

Observations of fish were approved by the Animal Welfare and Ethics Review Board in the University of Oxford's Department of Biology. The survey sent to fish traders was approved by the University of Oxford's Medical Sciences Interdivisional Research Ethics Committee (reference: R86176/RE002).

2.4 Results

2.4.1 Group-level Aggression

Counts of group-level aggression increased with stocking density (χ^2_3 = 7.067; p = 0.001; see **Figure 2.2**). Post-hoc analysis revealed this difference was driven by a significant increase in aggression from 9.39 ± 3.43 (mean chases ± SE) to 31.60 ± 3.43 between stocking densities of 4 and 10 (t = -5.582, d.f. = 24, adjusted p < 0.001). Indeed, no other pairwise comparisons of aggression across stocking densities were significant (4 *vs* 6: t = -2.400, d.f. = 24, adjusted p = 0.104; 4 *vs* 8: t = -2.686, d.f. = 24, adjusted p = 0.058; 6 *vs* 8: t = -0.286, d.f. = 24, adjusted p = 0.992; 6 *vs* 10: t = -2.182, d.f. = 24, adjusted p = 0.157; 8 *vs* 10: t = -1.896, d.f. = 24, adjusted p = 0.256).

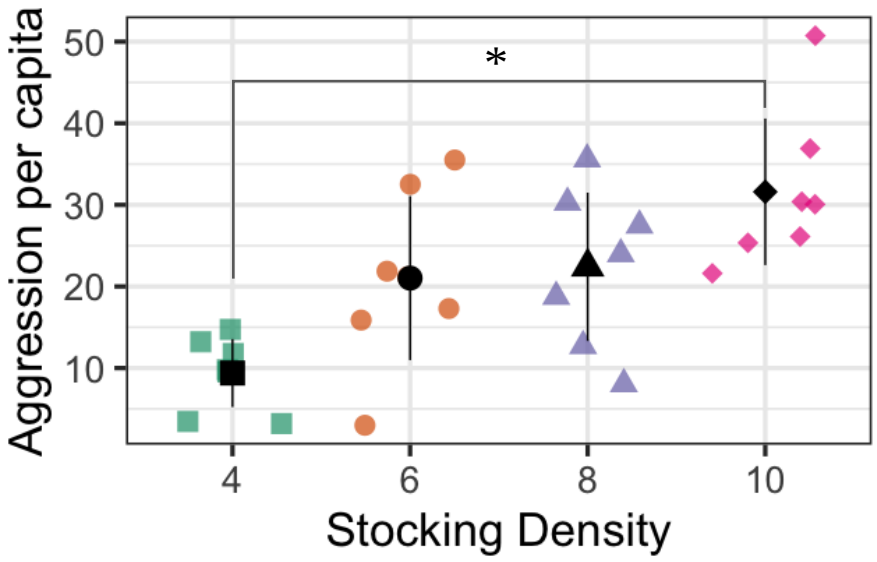


Figure 2.2: *per capita* aggression across stocking densities. Individual coloured points indicate, for each replicate group, the summed total of initiated aggression divided by the stocking density. Black points denote mean values ± 95% CI.

2.4.2 Inter-individual Variation in Aggression

With increasing stocking density, the observed variance in aggression that individuals initiated (out-degree) more often fell above the 97.5th percentile of the range expected under the null distribution (see **Figure 2.3a** and **Table 2.1**). Specifically, at stocking densities of 4, the observed variance exceeded the 97.5th percentile in 1 of 7 replicates; increasing to 7 of 7 replicates in stocking densities of 10. Overall, this indicated that individuals in more densely stocked groups were more likely to vary in their propensity for aggression and distribution of aggression among rivals.

Similarly, the observed variance in aggression that individuals received (in-degree) fell above the 97.5th percentile of the range expected under the null distribution least often within stocking densities of 4 (2 of 7 replicates) and most often within stocking densities of 10 (5 of 7 replicates). This indicated that individuals in more densely stocked groups were also more likely to vary in the amount of aggression they received and the number of rivals they received aggression from (see **Figure 2.3b** and **Table 2.1**).

Table 2.1: Significance (*p*-value) of the difference in the variance of in- and out-degrees relative to their respective null distributions for each replicate group across stocking densities. Significant *p*-values ($p < 0.05$) are shown in bold.

Replicate Group	**Stocking Density**							
	4		**6**		**8**		**10**	
	***p* out**	***p* in**	***p* out**	***p* in**	***p* out**	***p* in**	***p* out**	***p* in**
1	0.916	0.144	**<0.001**	0.088	0.470	0.196	**<0.001**	**<0.001**
2	0.888	0.800	**<0.001**	**0.006**	**0.006**	0.534	**<0.001**	0.068
3	0.066	0.120	**0.002**	**0.006**	**<0.001**	0.232	**0.010**	**<0.001**
4	0.660	0.472	0.668	0.054	0.148	0.244	**<0.001**	**0.040**
5	**<0.001**	**<0.001**	0.854	0.292	**0.006**	**0.006**	**0.004**	0.704
6	0.932	**0.012**	0.482	0.866	0.148	**0.020**	**<0.001**	**<0.001**
7	0.932	0.800	0.858	0.106	**0.010**	**0.002**	**<0.001**	**0.008**

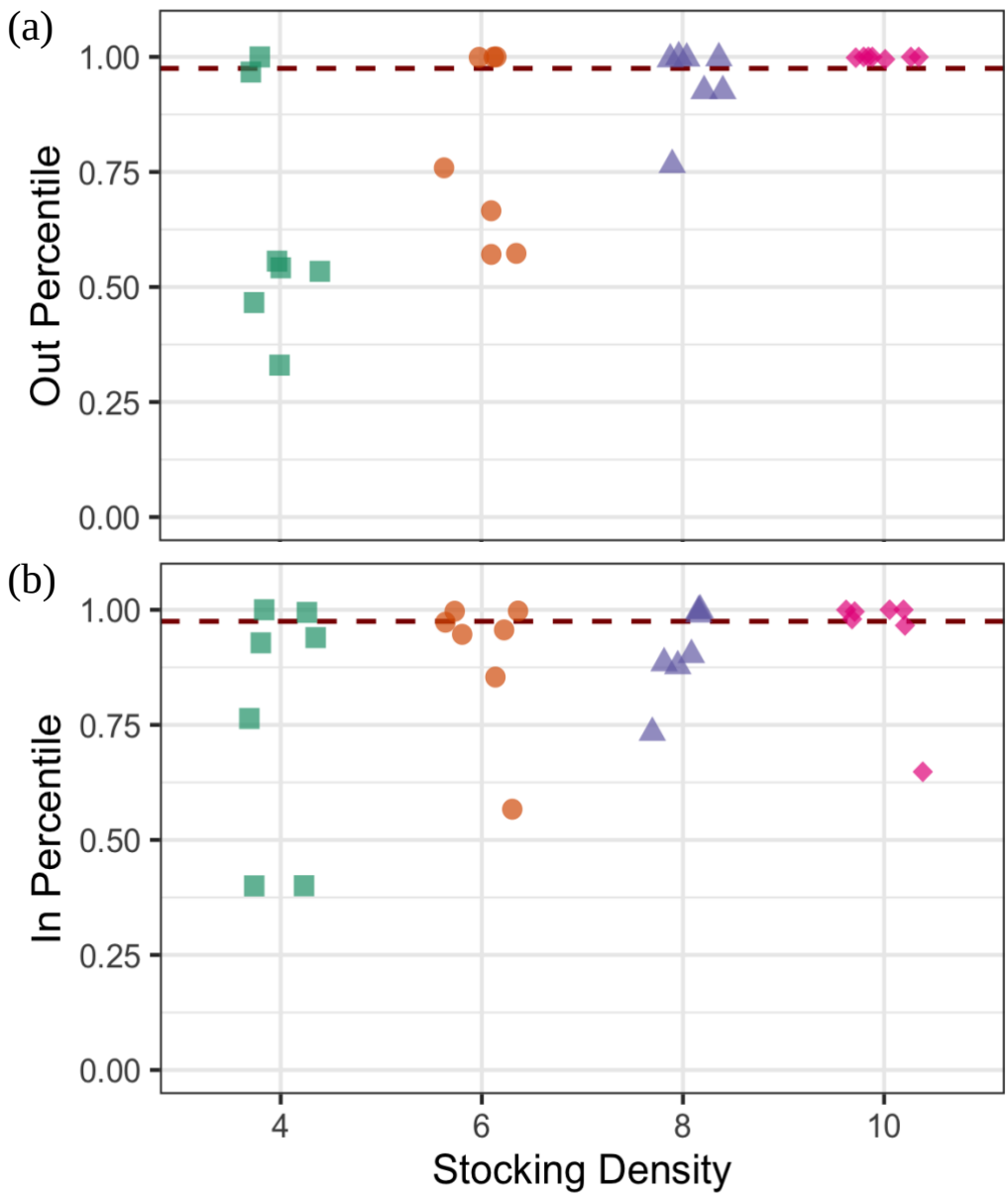


Figure 2.3: Points showing the percentile of the null distribution of that the observed variance in (a) out-degree; and (b) in-degree for each replicate group across stocking densities. The dashed red line indicates the 97.5th percentile which is the upper bound of the 95% range of the null distribution. Values above this dashed red line were considered to be significantly non-random.

2.4.3 The Role of Body Size

We found a significant, positive relationship between body size and counts of initiated aggression across stocking densities, indicating larger individuals were generally more aggressive (χ^2_1 = 3.978; p = 0.046; size difference * stocking density: χ^2_1 = 2.581; p = 0.461).

Within dyads where aggression occurred, we found that the tendency for the larger individual to initiate aggression increased when the size difference between opponents was greater. However, this effect was only apparent within stocking densities of 4 and 10, leading to a significant interaction effect (size difference * stocking density: χ^2_3 = 17.593; $p < 0.001$; see **Figure 2.4** and **Table 2.2a**).

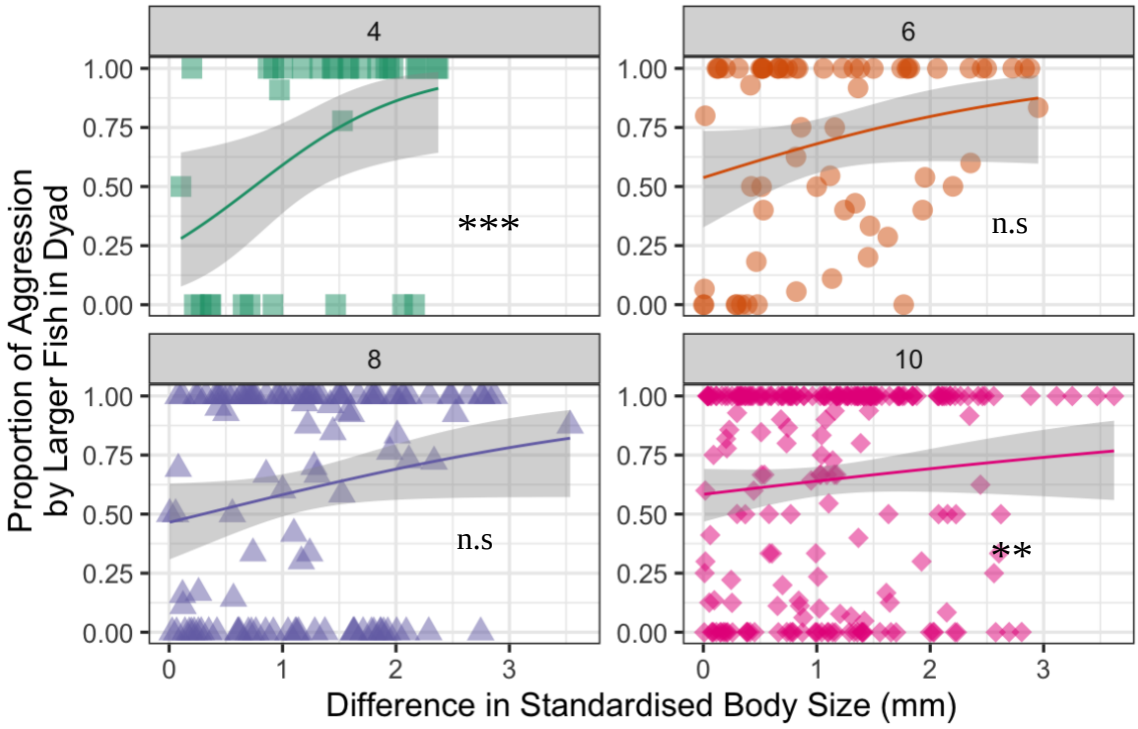


Figure 2.4: The relationship between the proportion of aggressions initiated by the larger individual within a dyad and size asymmetry (the absolute difference in standardised body size (mm)) within dyads across stocking densities of 4, 6, 8 and 10. Regression slopes from a binomial model with ±95% confidence intervals are shown. Significant deviations in the slope of each regression line from 0 are shown for each stocking density (n.s.: $p > 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Table 2.2: Post-hoc estimates of the regression slope for each stocking density in models investigating: (a) the proportion of aggression initiated by the large individual in dyads with increasing size asymmetry; (b) the occurrence of aggression in dyads with increasing size asymmetry. *z*-statistics and *p* values are shown. Significant *p*-values ($p < 0.05$) are indicated in bold.

Stocking Density	**(a) Proportion of Aggression**		**(b) Occurrence of Aggression**	
	z	***p***	***z***	***p***
4	5.222	**<0.001**	1.086	0.277
6	1.135	0.256	-1.373	0.170
8	0.933	0.351	0.783	0.434
10	2.789	**0.005**	-2.571	**0.010**

When all potential dyads were considered, we found aggression was most likely to occur in dyads containing individuals of a similar size in stocking densities of 6 and 10 while an opposite trend was observed in stocking densities 4 and 8. This led to an interaction effect between size difference and stocking density ($\chi^2_3 = 7.823$; $p = 0.050$; see **Figure 2.5** and **Table 2.2b**). However, power analyses using the estimated slope of the regression line for stocking densities of 10 (-0.542) indicated the power to detect a relationship between aggression and size asymmetry in stocking densities of 4, 6 and 8 did not exceed the commonly used 80% threshold (power in stocking densities of 4: 20.90%; 6: 28.40%; and 8: 72.50%).

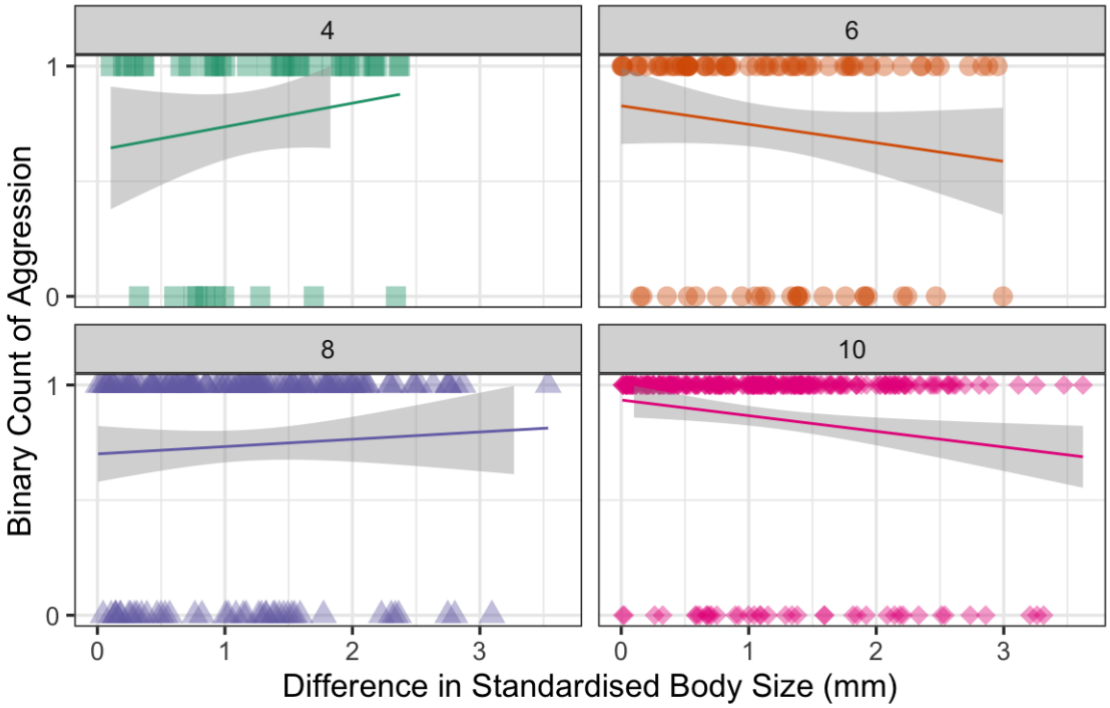


Figure 2.5: The relationship between the binary occurrence of aggression within a dyad and size difference (the absolute difference in standardised body size (mm)) within dyads across stocking densities of 4, 6, 8 and 10. Regression slopes from a binomial model with ±95% confidence intervals are shown to indicate the direction of the relationship between axes, though there was only statistical power to detect an effect for stocking densities of 10.

2.4.4 Survey Outcomes

We surveyed ornamental fish traders to understand the frequency with which stocking fish at high densities is used to manage aggression. Overall, 7 of 10 survey respondents reported stocking fish at high densities, noting this was particularly useful within cichlid species from the Haplochromini tribe. Recommended 'high stocking densities' for this tribe (which includes *L. ocellatus*) were 10-

12 individuals *per* 250 litres. In addition to reduced aggression, reported benefits of stocking fish at high densities were reduced mortality and observations that aggression appeared to be more evenly dispersed across individuals within tanks. In addition to (or instead of) stocking fish at high densities, respondents also reported introducing environmental complexity (e.g. plants, rocks), segregation of the sexes, and combining multiple species as methods for reducing aggression.

2.5 Discussion

Stocking individuals at high densities is a commonly used tool for reducing group-level aggression in captive species. However, there is little understanding of the changes in individuals' propensity for, and distribution of, aggression that underlie this group-level trend. In this study, we found no evidence for declining *per* capita aggression in male *L. ocellatus* with increasing stocking density within the range of our experimental manipulation. At the individual level, we found a positive relationship between body size and counts of initiated aggression that held across stocking densities. In stocking densities of 4 and 10, the larger individual within dyads initiated proportionally more aggression as the size difference between opponents increased. This was not the case for intermediate stocking densities of 6 and 8, suggesting aggression was more equally distributed within dyads of these groups. Finally, in stocking densities of 10, instances of aggression appeared to be mostly confined to dyads where both opponents were large. Overall, considering patterns of aggression at both the group and individual level uncovered a nuanced effect of the competitive environment on the decision-making guiding aggressive behaviours.

In this study, we predicted aggression would show a concave relationship with increasing stocking density. Such a relationship should emerge when the benefits of aggression exceed the costs in

lower, but not higher, stocking densities. Indeed, at higher stocking densities, the net benefits of aggression may be low when excluding each opponent has a proportionally small effect on shrinking the pool of competitors (Grant 1993). In our study, we did not find a concave relationship of *per* capita aggression across stocking densities. This may indicate that the range of stocking densities we explored was too narrow. Anecdotal advice[3,4] on stocking densities for *L. ocellatus* ranges from 3-6 fish *per* 75 litres, depending on the floor space provided by the tank dimensions. Further, the results of our survey revealed stocking recommendations of 10-12 fish *per* 250 litres for the Haplochromini tribe (which includes *L. ocellatus*). Considering this, we suggest the stocking densities considered in this study (4-10 fish *per* 40 litres) encompass a range from low to high. However, stocking recommendations often pertain to mixed-sex breeding groups, where the presence of resources (mates, breeding substrates) may increase the intensity of competition, facilitating a concave change in aggression within a lower range of stocking densities.

The absence of contestable resources may have increased the range of stocking densities across which a concave change in aggression was expected to occur. However, there was no suggestion of chasing transitioning towards a plateau with increasing stocking density, as averaged *per capita* aggression showed a significant increase between stocking densities of 4 and 10. Group-level aggression in *L. ocellatus* under these conditions may instead increase monotonically with competitor density if the associated benefits always exceed the costs (Sirot 2000). Alternatively, some species may lack the behavioural plasticity to reduce aggressive behaviour, even after the net benefits of competition decline past zero (Duckworth 2010). Similar increases in aggression with competitor density have been previously reported in other species, including chickens (Al-

[3] https://www.cichlid-forum.com/threads/lamprologus-ocellatus-tank-requirements.215821/?post_id=1502755&nested_view=1#post-1502755

[4] https://www.cichlid-forum.com/threads/lamprologus-ocellatus-gold.456218/?post_id=3153162&nested_view=1#post-3153162

Rawi and Craig 1975), pigs (Weng, Edwards *et al.* 1998) and house sparrows (*Passer domesticus*) (Johnson, Grant *et al.* 2004). As we conducted this study with an interest in its applications for improved animal welfare, suggestions for observations at higher stocking densities to confirm the absence of a concave relationship, and to quantify the costs of competition to individuals, may be difficult to justify from a welfare perspective.

Fishkeeping practice is often informed by the outcomes of aggression, such as mortality, as behavioural observations may be unfeasible within a commercial setting (see 2.4.4 Survey Outcomes). In our study, we chose stocking densities within which mortality (resulting from aggression) was not considered a realistic outcome. However, alternative measurements of stress (e.g. cortisol levels, Earley, Edwards *et al.* 2006) or injury (e.g. fish scale loss, Neat, Taylor *et al.* 1998), may be considered in future studies to assess whether the costs of receiving aggression decline in higher stocking densities, despite no decrease in the amount of aggression initiated. This may reveal a concave relationship, for example, if each occurrence of chasing is itself more costly (e.g. longer, more likely to result in injury) in intermediate stocking densities. Alternatively, a concave relationship between aggression and stocking density may only be apparent for more injurious (costly) behaviours that occur between these cichlids, such as biting and mouth wrestling. Indeed, in fig wasps (*Phylotrypesis pilosa*), the frequency of fights that resulted in severe injuries peaked within a mid-range of male densities (Murray 1987). In our study, we considered only 'successful' chases (i.e. chases that caused the recipient to retreat) as other aggressive behaviours occurred too infrequently over the 30-minute observation period for comparisons to be made across stocking densities. Future studies with a longer observation time may be useful in testing proportional changes in types of aggressive behaviour across stocking densities.

Underlying the increases in group level aggression; network analyses showed as stocking density increased, individuals varied more in the amounts of aggression initiated and received (i.e. observed variance of in- and out-degrees fell within respective null distributions less often at higher stocking densities). Considering that social networks for higher stocking densities are comprised of more nodes, and hence have greater power to detect non-random patterns of aggression, this result is perhaps unsurprising. However, additional differences in the initiation and distribution of aggression across stocking densities (described below) indicate patterns of individual behaviour were not merely a consequence of statistical power.

Across stocking densities, larger individuals initiated significantly more aggression compared to smaller individuals. As we considered 'successful' chases that necessitated a retreat by recipients, this result supports previously established relationships between body size and RHP in fish (Earley and Hsu 2013). Additionally, there was more variance between individuals in the amount of aggression initiated at higher stocking densities. Larger variance between individuals may drive a stronger relationship between body size and the propensity to initiate aggression. As such, we may expect this to result in a stronger association between body size and counts of initiated aggression in higher stocking densities. However, there was no evidence of an interaction effect between body size and stocking density to support this.

In stocking densities of 4 and 10, larger individuals in dyads became increasingly likely to initiate chases as the size difference between opponents increased. On the other hand, in intermediate stocking densities of 6 and 8, the size difference within dyads did not predict the proportion of chases initiated by the larger opponent. Thus, although body size and aggression are positively related, larger individuals do not become more aggressive towards increasingly smaller opponents in stocking densities of 6 and 8. This suggests that aggression in intermediate stocking densities is

more evenly distributed within dyads and may be particularly beneficial for small fish, if chases from much larger individuals are more likely to result in injury (Briffa and Sneddon 2007). Responses to our survey indicated that increasing stocking densities are considered to improve welfare through aggression becoming more dispersed across individuals. We suggest this outcome is most effectively encouraged through intermediate stocking densities (within the context of this study) for *L. ocellatus*.

In stocking densities of 10, individuals were significantly more likely to be aggressive to rivals of a similar body size. As opponents become more similar in (body) size, increases in aggression are expected (e.g. Enquist and Leimar 1983, Evans and Shehadi-Moacdieh 1988, Brunkow and Collins 1998). In combination with our findings that: (a) larger individuals are more aggressive; and (b) variance in aggression initiated and received increases with stocking density, these results suggest that instances of chasing are confined among the largest individuals in stocking densities of 10. This result is consistent with reports of frequent aggression between large pigs at high stocking densities (Andersen, Nævdal *et al.* 2004), but contrasts with findings in domestic chickens where, although aggression is initiated by a minority of birds, this aggression is distributed indiscriminately across rivals (Estevez, Keeling *et al.* 2003). Stocking fish at high densities may thus be detrimental for larger individuals, if they accumulate injuries through continual aggression. However, if larger individuals are better able to endure the costs of aggression – and most aggression occurs between these competitors – higher stocking densities may instead improve the overall condition of fish stocks, justifying common fishkeeping practice (Johnstone and Norris 1993).

In this study, there was no significant relationship between the occurrence of aggression and size asymmetry in stocking densities smaller than 10. This appeared to have been driven by a lack of

statistical power to detect such a relationship within smaller groups. Further, while variance in body size did not significantly differ between stocking densities (linear regression: $F_3 = 1.860$; $p = 0.167$), differentials of body size between opponents occupied a broader range as group size increased (see x axes of **Figures 2.4** and **2.5**). Smaller size differentials may have allowed relationships between aggression and size asymmetry to be more clearly detected or may simply have allowed more opportunities for aggression between large individuals, at higher stocking densities (Brunkow and Collins 1998).

It is interesting to note that for some stocking densities (4 and 8) the direction of the relationship between aggression and size difference within dyads, although not significant, opposed that found for stocking densities of 10. Specifically, in stocking densities of 4 and 8, aggression within dyads became more likely as the size difference between opponents increased. Across species, individuals differ in their distribution of aggression towards conspecifics (Hobson, Monster *et al.* 2021). In the majority of reported species, individuals distribute aggression indiscriminately towards weaker rivals, but in a significant minority of species (22%), individuals distribute more aggression towards either the weakest opponent ('bullying'), or closely matched competitors (Hobson, Monster *et al.* 2021). Our study suggests that the distribution of aggression within a species may be sensitive to the density of competitors in the surrounding social environment. Increasing the sample size for our study could confirm this suggestion for *L. ocellatus*, by increasing the statistical power to address whether aggression is distributed towards much weaker rivals in some (lower) stocking densities. In stocking densities of 4, where larger individuals initiate relatively more aggression (*vs* smaller individuals), the occurrence of bullying may be especially costly for small fish if body size predicts individuals' abilities to both inflict and withstand aggression (Maynard Smith and Brown 1986).

2.6 Conclusion

In this study, we investigated changes to aggressive behaviour across stocking densities at both a group and individual level. We show that, at higher stocking densities, group level aggression increases, contradicting theoretical predictions and fish keeping advice which suggest the occurrence of competition should follow a concave pattern. At the individual level, variance in the amount of aggression individuals initiated and received increased across stocking densities. This variance was driven by larger individuals becoming increasingly aggressive towards other large individuals in densely stocked tanks. While larger fish may better withstand the costs of receiving aggression, stocking fish at intermediate densities – where aggression is more broadly distributed – may be most effective in improving individual welfare in *L. ocellatus*. In our survey, respondents also suggested introducing environmental complexity (e.g. plants) as an additional method for managing aggression. While logistical constraints (i.e. ease of observation) necessitated the removal of environmental complexity in this study, future studies should consider the combined effects of changing the physical and competitive environment to reduce aggression in this, and other, species. In the next Chapter, I will explore this by investigating the effects of environmental complexity and sex ratio on competitive behaviours in red junglefowl.

Appendix A: Supplementary Material for Chapter 2

Table A.1: List of questions for a survey investigating methods for reducing aggression in commercially kept fish.

Question	Answer Format	Conditional Outcome
Do you attempt to manage aggression by stocking fish at high densities?	Yes / No	If 'No', go to final question
By how much do you increase the density of fish in tanks as a means of managing aggression (e.g. 1-2 additional fish per 10 fish)? Please provide this information for each species or type of fish (e.g. Malawi cichlids).	Short answer	*NA*
What best describes your reason for using increasing stocking density as a method to reduce aggression?	Multiple choice: Personal experience, published advice (online or in print), professional advice, other (please specify)	*NA*
Have you noticed a reduction in aggression between fish as a consequence of increasing stocking density? Briefly describe your observations.	Short answer	*NA*
Briefly describe what other methods (if any) you use to reduce aggression among fish?	Short answer	*NA*

Chapter 3: *Effects of adult sex ratio and environmental complexity on competitive behaviours and space use in red junglefowl*

Hannah Ogden, Shreyas Pai, Eleanor Bath, Jonathan Green & Tommaso Pizzari

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Author contributions: Shreyas Pai and Tommaso Pizzari conceived of the study. Shreyas Pai and I designed the study and collected the data. I analysed the data and wrote the manuscript. The chapter was edited to incorporate comments from Eleanor Bath, Jonathan Green and Tommaso Pizzari.

3.1 Abstract

Adult sex ratio and environmental complexity are key ecological factors that influence patterns of sexual behaviours by modulating the strength of sexual selection and sexual conflict. For males, an increase in either the proportion of females in the population or the structural complexity of the habitat is predicted to lead to a reduction in intrasexual aggression over access to females, as a result of increased mate availability and decreased encounter rate respectively. Here, we test these predictions in red junglefowl (*Gallus gallus*) flocks by comparing intra- and intersexual behaviours and space use under different sex ratios (female biased or even) and levels of environmental complexity. We find that temporal patterns of male dominance behaviours varied with sex ratio, with males in female biased flocks crowing more in the morning and males in even flocks flapping

their wings less in the evening. A reduction in some male aggressive behaviours was also observed in female biased flocks where male competition over mating opportunities is presumably reduced. We found little evidence for an effect of environmental complexity on competitive behaviours, with the exception of wing flapping, which was related to dominance rank in simple, but not complex, environments. Finally, we observed a reduction in courtship and dominance behaviours by males and an increase in time spent in the centre of the arena by females over successive days, consistent with a decline in sexual interest due to increasing familiarity. Taken together, our results reveal that male investment in aggression is sensitive to both adult sex ratio and environmental complexity, though effects were context-dependent and not always in the predicted direction. Integrating information about the social environment, including sex ratio and environmental complexity, is thus likely to be important for predicting optimal allocation by males to mate competition.

3.2 Introduction

Sexual selection is the evolutionary process by which certain individuals gain a reproductive advantage over other individuals of the same species and sex through improved competitive and/or fertilisation success (Darwin 1871). Ecological factors, including the operational sex ratio (OSR; the ratio of sexually active males to fertilisable females at a given time; Emlen 1976) and complexity of the environment modulate the strength of sexual selection (Emlen and Oring 1977, Janicke and Morrow 2018). Across ecological landscapes, varying intensities of sexual selection should be reflected in sexual behaviours, including the extent of male-male competition over females and the degree of female choosiness over mating opportunities (Bateman 1948).

In species where male mating rates are constrained by the availability of receptive females, a more male biased OSR (i.e. diminishing numbers of females *per* male) should increase the intensity of sexual selection (Janicke and Morrow 2018). As the number of receptive females within a population declines, males will compete more aggressively for increasingly limited mating opportunities (Weir, Grant *et al.* 2011) and dominant males may be more effective in monopolising access to females (Emlen and Oring 1977, Clutton-Brock and Parker 1992). By modulating intrasexual competition, an increasingly male biased OSR should heighten the severity of sexual conflict as females undergo greater levels of sexual harassment, including courtship and coercive mating attempts, with negative consequences for female fecundity and lifespan (Clutton-Brock and Parker 1995, Kvarnemo and Ahnesjo 1996, Lovlie and Pizzari 2007, Weir, Grant *et al.* 2011, Chuard, Brown *et al.* 2016).

Under a constant OSR, varying environmental complexity may alter patterns of sexual selection, with implications for the expression of inter- and intrasexual behaviours. For example, less

efficient mate guarding (e.g. in the yellow-breasted chat, *Icteria virens*; Mays and Ritchison 2004), less efficient female mate choice (e.g. in three-spined sticklebacks, *Gasterosteus. aculeatus*; Candolin, Salesto *et al.* 2007), and a lower reproductive skew (e.g. *G. aculeatus*; Candolin 2004) can occur when dense vegetation diminishes visual contact between individuals and shifts the strength and direction of sexual selection (see also Candolin, Salesto *et al.* 2007, Malek and Long 2019, Wilgers, Colton Watts *et al.* 2022). In addition, reduced visual contact introduced by a complex environment may decrease encounter rates, lowering instances of intrasexual aggression and courtship interference (Baird, Patullo *et al.* 2006, Hibler and Houde 2006). Alternatively, when more densely vegetated habitats impede predation efficiency, this may instead encourage more conspicuous sexual behaviours, such as courtship, if natural selection for crypsis is weakened (Endler 1987, Michelangeli, Tuomainen *et al.* 2015). Finally, when intersexual encounter rates and male investment into sexual behaviours are modulated by the complexity of the environment, opportunities for female harm – and therein sexual conflict – may too depend on the influence of this ecological factor (Malek and Long 2019).

While OSR and environmental complexity may both alter sexual behaviours, there has been little consideration of how these factors interact to modulate processes of sexual selection. Despite this, sex-specific responses to environmental heterogeneity can lead to natural covariance between these ecological factors (Banks, Piggott *et al.* 2007). For instance, in certain killifish (*Nothobranchius* spp.) populations, males are more colourful than females and preferentially seek out more vegetated sites where the risk of predation is reduced, resulting in variation in the adult sex ratio over fine scales (Reichard, Polačik *et al.* 2014). Work has recently begun to address the potential interaction between environmental complexity and OSR, though no effect of these ecological factors was found on morphology and heterozygosity in a study on mosquitofish

(*Gambusia holbrooki*) (Head, Kahn *et al.* 2016). However, further work on additional species is required to fully elucidate the influence of these ecological factors on a broader range of traits, including inter- and intrasexual behaviours.

While changes to OSR and environmental complexity may alter patterns of sexual behaviours within a population, such effects are unlikely to remain constant over time. With cumulative matings, sperm reserves are depleted in males and accumulated within females, leading to lower male mating propensity and increased female resistance to mating (Lovlie and Pizzari 2007). Increased female resistance should be reflected by a decline in inter- and intrasexual behaviours as males are less inclined to compete for, court, and mate with less receptive females. However, these temporal declines may be slowed if high sperm competition encourages male remating to defend paternity (Parker, Ball *et al.* 1997). Thus, when sexual selection is more intense (within a male biased OSR or less complex environment), cumulative sexual behaviours may reach higher peaks and decline more slowly over time. The time-dependency of mating strategies can also vary in response to the reproductive cycle, such that peaks in sexual activity correspond to increases in fertilisation success (e.g. Domb and Pagel 2001). This time-dependency may interact with the OSR if females anticipate intense harassment during these peaks and alter their behaviour to mitigate this (Lovlie and Pizzari 2007). Overall, as sexual behaviours are expected to vary over time in response to OSR and environmental complexity, consideration of these temporal effects is required to fully elucidate the influence of these ecological factors.

In this study, we experimentally investigate the independent and interactive effects of ASR (Adult Sex Ratio) and environmental complexity on temporal patterns of sexual behaviours and intrasexual aggression in red junglefowl (*Gallus gallus*). As females in this species can store viable sperm for up to two weeks (Etches 1996), we assumed that all females were (perceived by males

to be) reproductively available, and thus that differences in ASR reflected changes in OSR (see Lovlie and Pizzari (2007) for a direct test of this). The dynamics of sexual selection in this species are well characterised (for a recent review, see Pizzari and McDonald 2019), and individual effects of ASR and environmental complexity on sexual, aggressive and dominance behaviours on red junglefowl and the closely related domestic fowl (*G. domesticus*) have previously been demonstrated. For example, reduced mating intensity and male harassment of females has been reported in pens containing visual obstructions that simulate a complex environment (Leone and Estévez 2008, McDonald 2014). Additionally, sexually immature fowl have shown an increased propensity to occupy more central spaces in environmentally complex pens where the risk of agonistic interactions with conspecifics is reduced (Cornetto and Estevez 2001). Once sexually mature, females may alter space use to facilitate the avoidance of harassment, for example by spending more time perching, as suggested by (Carleial, McDonald *et al.* 2019). Under more male biased ASRs, female fowl have been shown to adjust daily mating patterns to solicit copulations in the mornings, when insemination is less likely to lead to fertilisation and sexual harassment is concomitantly lower (Gracewski and Scott 1943, Parker 1945, Lovlie and Pizzari 2007). Whether changes to the ASR interact with environmental complexity to modulate sexual behaviours and intrasexual aggression in fowl has yet to be explored, however.

We predicted that intersexual behaviours, including male courtship of females and mating, and an intrasexual behaviour (male-male aggression) should show a reduced intensity and faster temporal decline in flocks with a female biased sex ratio or inhabiting a more complex environment. Further, when a reduced intensity of sexual behaviours translates to lower levels of female harassment, we predicted that females should alter their space use by perching less and spending more time in the central floor of aviaries, particularly in the evening when fertilisation success is most likely.

Finally, we predicted that increased environmental complexity would have greater scope to relax sexual selection in more male biased sex ratios, where inter- and intrasexual behaviours are more intense. As such, we expected any two-way interaction effects to be driven by a stronger influence of environmental complexity in flocks with more males *per* female.

3.3 Methods

3.3.1 Study Species

In the wild, red junglefowl live in small groups of 2-14 individuals with flocks often containing more females than males (average 0.63 females:males (range 0.14-4); McBride, Parer *et al.* 1969, Sullivan 1991, Collias and Collias 1996). Under even a moderately female biased OSR, however, the potential reproductive rate of males can be constrained by the sexual receptivity of females, who lay on average 8 eggs *per* clutch, with up to 3 clutches *per* year (Collias and Collias 1996). Males are therefore under strong sexual selection and aggressively compete with one another, with outcomes of aggression informing the order of dominance hierarchies that dictate priority of access to mating opportunities (Banks, Wood-Gush *et al.* 1979). Males may advertise and maintain social rank with conspicuous signals, such as crowing and wing flapping (male vigorously brings wings together behind his back), which are performed more frequently by males of higher ranks (Fessler, Zuk *et al.* 2001). Although dominant males receive the majority of mating opportunities, females are polyandrous and may occasionally mate with low-ranking males. Polyandry results in sperm competition and provides an incentive for males to remate the same female.

Female red junglefowl actively solicit matings from preferred mates by crouching in front of them to facilitate mounting. Though solicitation is generally rare, its occurrence should vary across time

and in response to ecological factors, such as sex ratio (Lovlie and Pizzari 2007). To counteract changes in female solicitation, males may coerce resistant females into mating to prevent missed reproductive opportunities.

3.3.2 Experimental Procedure

Experiments were conducted on a captive population of red junglefowl at the John Krebs Field Station of the University of Oxford in Wytham, UK, between July and August 2021. This population was established in 2006 and founded from captive populations in Sweden. All birds are housed in outdoor aviaries, individually marked with darvic and metal rings and habituated to human presence.

Observations of inter- and intrasexual behaviours and space use were conducted in flocks of six red junglefowl with either an 'equal' (three males and three females) or 'female biased' (two males and four females) ASR (hereafter 'sex ratio'). In total, 12 replicate flocks (5 with an 'equal' sex ratio and 7 with a 'female biased' sex ratio) were observed. All flocks were exposed to 'complex' (three semi-opaque barriers, hereafter 'barriers', assembled in pens; see **Figure 3.1**) and 'simple' environments on alternating days. All pens contained wooden pallets that were leant against the aviary wall creating an additional space that females used to shelter from male harassment (personal observation).

For each flock, environmental complexity ('simple' or 'complex') was randomly assigned on the first day of trials and varied sequentially every 24 hours across 4 days of observation. Birds in each trial were thus exposed to two days of 'simple' and two days of 'complex' environments. Environmental complexity was altered one hour before observations began to ensure that behaviours observed were not due to disturbance caused by the erection or removal of barriers.

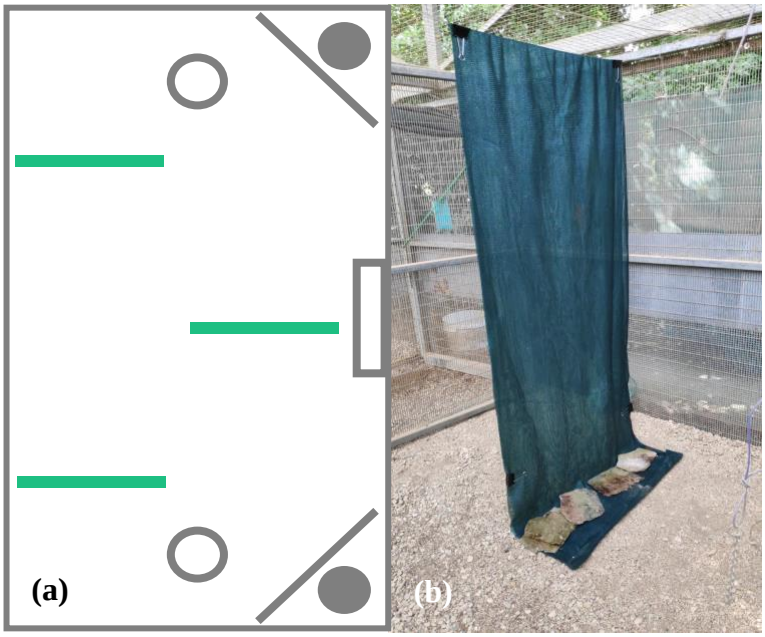


Figure 3.1: (a) Set-up of the experimental aviaries. Aviaries were 3.3 x 6.5 x 1.9 metres and contained two feeders (open circles), two drinking containers (closed circles), and multiple perching spaces (two perches, grey line; and one wooden palette, grey box). 3 barriers (green rectangles) were present in 'complex' but not 'simple' environments. (b) Green shade netting was hung in two layers from washing line to create 90 x 185cm translucent barriers. The small space between the top of the barriers and aviary ceiling (5cm) prevented the barriers from providing an additional perching space for birds.

Males and females were housed in single-sex enclosures for 48 hours before trials commenced, allowing for standardised familiarisation among individuals (Craig, Biswas *et al.* 1969, D'Eath and Keeling 2003), replenishment of male sperm stores (Parker, McKenzie *et al.* 1942), and to prevent increased female resistance as a result of recent mating (Pizzari, Cornwallis *et al.* 2003). All individuals were expected to be sexually receptive following this period of sexual rest, thus allowing changes in the ASR to correspond with changes in the OSR (Lovlie and Pizzari 2007). Females were moved into experimental pens 24 hours before trials commenced and observed for

one evening and morning to collect information on female space use (see Data Collection) in the absence of males. Due to a constraint on the number of birds available, male birds were reused up to 3 times across trials (average 1.17) and female birds were reused up to 2 times (average 1.43). No birds were used in consecutive trials. All birds were between the ages of 1 and 6 years (mean male age: 3.897 (± 0.434 SE) years; mean female age: 3.279 (± 0.351) years).

Flocks were observed twice daily in the morning and the evening. Observations of two flocks (one of each 'sex ratio') were performed in parallel and the order in which flocks were observed was randomised each morning and evening. Each flock was observed in two 30-minute sessions, with a 30-minute break between sessions (during which the alternative flock was observed). This resulted in one hour of observation per flock each morning and evening. As sexual activity generally peaks in the early morning and evening (McBride, Parer *et al.* 1969), morning observations began one hour after sunrise (range 06:01-07:09 BST) and finished one hour before sunset (range 18:49-19:51 BST). Observations commenced on the evening of trial day 1 and finished on the morning of trial day 4. Each trial day thus comprised one evening and one morning observation, with 'environmental complexity' varying on the evening of each trial day.

3.3.3 Data Collection

Behavioural Observations

As flocks contained only six individuals, mating, courtship, and aggressive behaviours could be sampled *ad libitum* (Altmann 1974). Across a total of 110 hours of observations, 5,297 instances of behaviours were recorded. For all behaviours, the identities of birds were recorded.

All heterosexual mating attempts (successful and unsuccessful) were recorded. Mating attempts were considered successful when cloacal contact was observed or assumed to occur (when the male lowered his tail over the female's cloaca) (McDonald 2014). Female solicitation of mating rarely occurred (24 of 358 matings were solicited), and so variation in female solicitation in response to sex ratio and environmental complexity was not considered. For remaining unsolicited matings, male mating effort was recorded as: 'low' (male approaches female but female does not solicit mating, or male grabs female and female passively accepts mating), or 'high' (male grabs or chases female, female resists mating) (Lovlie and Pizzari 2007). Approximately 13% of mating attempts were 'interrupted' when the mating male was displaced by another male. When mating attempts were interrupted, mating effort was not recorded as it was difficult to gauge females' mating resistance. Information on male mating effort and female solicitation could not be recorded for two instances of mating as the onset of mating was not observed. All instances of courtship (where a male 'waltzes' by moving in a semi-circular path around a female's head while extending and fluttering his outer wing) between a male and female were recorded.

All counts of dominance behaviours (crows and wing-flaps) performed by each male were recorded. Additionally, all aggressive interactions between pairs of males were recorded. Aggression occurred whenever one male lunged, chased, pecked or waltzed towards another male, or when two males fought (Wood-Gush 1956).

The outcomes of aggression between males were combined with information on avoidances (a target male moves >1 body length within 10 seconds of being approached by an initiating male) to determine Elo scores within groups (Elo 1978). Elo scores were calculated to incorporate information on social rank into analyses of dominance behaviours (see Statistical Analysis) and to identify dominant males (i.e. the male with the highest Elo score within a group) for whom mating

skews could be calculated. Elo scores are based on the outcome (wins/losses) of dyadic interactions and the relative success of the competing individuals and can be ranked to infer the hierarchical structure of a group. For fights, losers were defined as the individual that retreated at least one body length from the other individual within 10 seconds. For all other aggressive interactions, it was observed that initiators almost never retreated from the target to whom they directed aggression (T. P personal communication; H. J. P. O personal observation). As such, 'winners' and 'losers' were considered to be the initiators and targets of interactions, respectively (see (Pasternack Murray 2022) for a similar classification). Elo scores were calculated using the 'EloRating' package in R (v.4.0.0) (Neumann, Duboscq *et al.* 2011, R Core Team 2013).

The order of dyadic interactions is important in determining Elo scores, but estimates may be unreliable when interactions are not randomly distributed over time. Thus, to increase robustness of dominance estimates, dyadic interactions were randomly ordered 1,000 times and Elo scores from each randomisation were averaged using the 'aniDom' package (v.0.46.11) (Sánchez-Tójar, Schroeder *et al.* 2018). Across all groups, the repeatability of ranked Elo scores across 1,000 randomisations was assessed, with a repeatability threshold of ≥0.8 indicating hierarchy estimates were robust and did not depend on the order of dyadic interactions (Sánchez-Tójar, Schroeder *et al.* 2018). This additionally implied that estimates of dominance rank were unlikely to change throughout the duration of each trial.

Space Use Measures

In addition to behavioural observations, scan sampling was performed every five minutes to collect data on female space use, namely perching and proximity to the aviary borders (hereafter 'border proximity') (Stanley, Liddiard Williams *et al.* 2018, McDonald, Spurgin *et al.* 2019). Each group was scanned on average 87 (range 53-96) times. Females were recorded as perching during scans

when they were on perches and on or behind wooden pallets. Females were recorded as being in close proximity to the aviary borders during scans if they were within one body length from the border.

As both perching and staying in close proximity to aviary borders may be alternative strategies to avoid male harassment, they were incorporated into a single measure of the proportion of scans females were on the central floor of pens (i.e. not perching or near aviary borders).

3.3.4 Statistical Analyses

General model structure

All statistical analyses were conducted in R (v.4.0.0) (R Core Team 2013). Unless stated otherwise, analyses were performed using generalised linear mixed models (GLMMs). GLMMs were initially fitted with a Poisson distribution and run with the 'lme4' package (Bates 2010). If GLMMs were found to be overdispersed (tested for with the 'performance' package; Lüdecke, Ben-Shachar *et al.* 2021) models were fitted with a negative binomial distribution and run with the 'glmmTMB' package (Brooks, Kristensen *et al.* 2017). All GLMMs contained fixed effects of environmental complexity ('complex' and 'simple'), sex ratio ('even' and 'female biased'), time of day (morning and evening), and trial day (days 1-4). Trial day was included as a factor rather than a covariate as temporal trends in sexual behaviours may be non-linear (e.g. Lovlie and Pizzari 2007).

Competition between more males for fewer females in the 'even' (*vs* 'female biased') sex ratio should increase the intensity of sexual selection and sexual conflict relative to the 'female biased' sex ratio, and, as such, the magnitude of the effect of environmental complexity is expected to be greater in this sex ratio. For this reason, a two-way interaction of sex ratio and environmental

complexity was included in all GLMMs. Additionally, daily patterns of sexual behaviours may be expected to vary across sex ratios. To explore this, a two-way interaction of sex ratio and time of day was incorporated into GLMMs. Finally, though an increase in male harassment of females may be expected in the evenings, the extent to which this alters behaviours and space use may vary depending on the environmental complexity. GLMMs were therefore fitted with a two-way interaction of environmental complexity and time of day.

Whole observation sessions were occasionally missed (one morning observation for one 'even' and one 'female biased' trial and one evening observation for another 'even' and 'female biased' trial) and so relevant data points for this trial day and time of day were not included within GLMMs. For one session (the morning of trial day 3 for one 'female biased' and one 'even' trial), each group was observed for only one 30-minute observation block. To account for this reduced observation time, an offset of the number of observation blocks contained within each trial was included in GLMMs. Offsets were transformed in accordance with the link-function of the GLMM which is specified for each model below.

All GLMMs contained a random effect of Replicate Trial ID as measures from the same replicate group were taken over multiple trial days across both environments ('simple' and 'complex'). As up to two trials were observed across the same days, Observation Date (the date of trial day 1) was included as an additional random effect. To prevent issues of singularity, random effects were removed from models if their effects were too low to be estimated (tested for with the 'performance' package; Lüdecke, Ben-Shachar *et al.* 2021).

To test whether predicted peaks in sexual activity (and related measures) on the first day of trials did not obscure the effect of sex ratio or environmental complexity, all models were re-run on a

subset of data that excluded trial day 1. The output of GLMMs both including and excluding trial day 1 are discussed in the Results.

Intersexual behaviour GLMMs

Counts of courting and mating (included attempted mating) performed by males were separately summed for the morning and evening of each trial day, then divided by the number of males within the group (as determined by the sex ratio). These values were used as response variables in GLMMs and indicated the average courtship and mating counts performed by males. Because averaged counts were non-integer and right skewed, these GLMMs were fitted with an inverse-link Gamma distribution.

To investigate mating effort, the proportion of all unsolicited matings that were 'high' effort (N_{high} / (N_{low} + N_{high})) for each morning and evening within trial days was entered as the response variable within a GLMM. This GLMM was fitted with a logit-link binomial-error distribution. As the frequency of mating may affect the effort that males expend, the GLMM was weighted by the number of matings that occurred in each observation session.

As an initial assessment of mating skew (i.e. the extent to which dominant males were able to monopolise matings) within each sex ratio, two one-sample Wilcoxon signed-rank tests were used. In each test, the proportion of matings achieved by the dominant male was compared against a hypothesised median that assumed all males shared matings equally (0.33 for 'even' sex ratios and 0.5 for 'female biased' sex ratios). For the 'even' sex ratio an exact *p*-value could not be computed as many proportional values were the same and could not be ordered within the Wilcoxon signed-rank test. To test whether mating skew varied with sex ratio and environmental complexity, the proportion of matings achieved by the dominant male each morning and evening within trial days

was entered as the response variable within a GLMM. As mating skew is a proxy of dominant males' ability to monopolise paternity, only successful matings were considered. The GLMM was weighted by the total number of successful matings that occurred in each observation session. In one 'female biased' trial, and in the 'complex' environment of one 'even' trial, no successful matings were observed, meaning that mating skew could not be calculated. Because the number of males varied across sex ratios, male mating skew for 'even' and 'female biased' trials were analysed in separate GLMMs. These GLMMs were fitted with a logit-link binomial-error distribution.

Intrasexual behaviour GLMMs

Males performed dominance related behaviours (crows and wing flaps) towards no discernible target. Counts of crows and wing flaps were therefore summed *per* individual for each morning and evening within trial days and entered as response variables in separate GLMMs. Additional GLMMs were run with a fixed effect of dominance rank to test whether positively predicted counts of crowing and wing flapping (previously shown by Fessler, Zuk *et al.* 2001). However, as the number of dominance rank levels reflected the number of males present in a flock, GLMMs were run separately for each sex ratio. As dominant males are expected to perform more crows and wing flaps, the effect of environmental complexity and time of day on these behaviours may depend on the social rank of the male. As such, GLMMs for each sex ratio contained two-way interactions between dominance rank and environmental complexity, and dominance rank and time of day. In one analysis ('even' sex ratio with trial day 1 excluded), very low variance in crowing activity by the lowest ranking males prevented the environmental complexity and time of day interaction term from being included in the model. All crowing and wing flapping GLMMs were fitted with a log-

link negative binomial distribution. Individual ID was included as an additional random effect in GLMMs as crows and wing flaps were measured at the individual level.

Intrasexual aggression between males mostly comprised of chases and lunges (38.2% and 39.3% of 280 counts of intrasexual aggression summed across trials respectively) and these were positively correlated across trials (Spearman's *rho*= 0.647, $p = 0.023$). Waltzing between males was also frequently observed (comprising 18.2% of all aggressive behaviours) but counts of waltzing were uncorrelated with lunging ($r_s = -0.264$, d.f. = 10, $p = 0.407$) and chasing ($r_s = -0.380$, d.f. = 10, $p = 0.223$) across trials. Separate GLMMs were therefore used to compare summed counts of chases and lunges and counts of waltzing. As pecks and fights occurred infrequently (1.1% and 3.2% of all aggressive behaviours, respectively) and were uncorrelated with other aggressive behaviours, these were not included in analyses of intrasexual aggression.

Combined counts of chases and lunges, and counts of waltzes between males, were separately summed for each morning and evening within trial days, then divided by $n - 1$ (where n indicates the number of rivals a male has within a group, as determined by the sex ratio). These values were used as response variables in GLMMs and indicated average counts of two measures of aggression between males. As both averaged counts were non-integer and right skewed, these GLMMs were fitted with an inverse-link Gamma distribution.

Space use GLMMs

Perching and border proximity were recorded as binary measures (yes/no) *per* female for each scan during an observation. These measures were then combined into an overall binary measure of presence in the central floor of pens ('yes' indicates a female is neither perching nor nearby the aviary border) *per* female during each scan. A GLMM for space use was fitted with a logit-link

binomial-error distribution. Individual ID was included as an additional random effect as space use was measured at the individual level. Observation block was initially included as a random effect (as scans during 30-minute observation periods may show temporal autocorrelation) but was removed as it explained very little variance.

Testing for age effects

Increasing age has been previously linked to a decline in mating frequency and mating success in male *G. domesticus* (Dean, Cornwallis *et al.* 2010), and reduced fecundity and altered space use (increased perching) in *G. gallus* females (McDonald, Spurgin *et al.* 2019). To investigate whether the age of males and females within groups were related to any behaviours and patterns of space use in this study, additional variations of all GLMMs were run with covariates: (i) female age; (ii) male age; or (iii) both female and male age. For GLMMs with response variables that summarised behaviours across multiple individuals, male and female ages were averaged across individuals of each sex within a trial. For GLMMs where each response variable was a measure of the behaviour or space use of a single individual, the age of the individual was entered as the age covariate for that sex (for the opposite sex, the average age across individuals was entered as a covariate). Models that were significantly improved ($\Delta AIC \leq 2$) by adding one or more covariates are presented in the Results in place of the simpler model without these covariates.

Model outputs

The outcome of GLMMs were analysed with a Wald χ^2 test using the *Anova* function from the 'car' package (Bolker, Brooks *et al.* 2009, Fox, Weisberg *et al.* 2012). A Type III Wald χ^2 test was specified as GLMMs included two-way interactions (Speed, Hocking *et al.* 1978). The 'emmeans' package was used to conduct post-hoc analyses (Lenth, Singmann *et al.* 2019).

3.3.5 Ethics

This study was carried out in accordance with the United Kingdom home office legislation (Home office license 30/2418). All work was approved by the Departmental Animal Welfare Ethical Review Body.

3.4 Results

3.4.1 Intersexual Behaviours

Average counts of male courtship showed a significant decline across trial days ($\chi^2_3 = 53.177$, $p < 0.001$; see **Figure B.1** in Appendix B). Post-hoc analysis indicated this was driven by high numbers of courtship on trial day 1 relative to other days (trial day 2*: z* = 0.047, adjusted $p < 0.001$; trial day 3*: z* = 0.041, adjusted $p < 0.001$; trial day 4*: z* = 0.051, adjusted $p < 0.001$). When trial day 1 was removed from analyses, counts of courtship did not vary significantly across trial days ($\chi^2_2 = 0.065$, $p = 0.968$). There was no effect of sex ratio, environmental complexity, or time of day on courtship counts in analyses both including and excluding trial day 1 (see **Table 3.1**).

Average counts of male mating attempts did not significantly vary across environmental complexity and sex ratio nor over time (trial day and time of day; see Table 1). Male mating effort (i.e. the proportion of matings unsolicited by females) was significantly higher in groups where females were older on average. When the effect of female age was controlled for, male mating effort was shown to be unaffected by environmental complexity and sex ratio, and also did not vary with time (trial day and time of day). Findings for mating count and mating effort were not significantly altered when trial day 1 was excluded from analyses (see **Table 3.1**).

Within sex ratios, mating skew towards the dominant males did not significantly differ across 'simple' or 'complex' environments or over time (trial day or time of day) (see **Table 3.1**). Dominant males obtained 70.8% (± 0.1% S.E.) of successful matings in 'even' sex ratios (3 males, 3 females), a significantly higher proportion than expected by chance (V = 227, $p < 0.001$). Dominant males obtained 56.0% (± 0.1% S.E.) of successful matings in 'female biased' sex ratios (2 males, 4 females), which was not significantly more than expected by chance ($V = 64$, $p = 0.484$).

Table 3.1: Intersexual (mating and courtship) behaviours. For each GLMM, a summary statistic (χ^2), degrees of freedom (df) and *p*-values are shown. Significant results ($p \leq 0.05$) are indicated in bold. [1] and [2] Indicate models where respective random effects of Observation Date or Replicate ID explained very little variance and were removed.

Response variable	**Fixed effect/covariate**		***All days***			***Day 1 Excluded***		
			χ^2	**df**	***p***	**χ^2**	**df**	***p***
Mating Count[1]	Sex Ratio		0.245	1	0.621	0.304	1	0.581
	Environmental Complexity		0.543	1	0.461	0.553	1	0.457
	Time of Day		2.156	1	0.142	1.580	1	0.209
	Trial Day		4.783	3	0.188	0.954	2	0.621
	Sex Ratio * Environmental Complexity		0.962	1	0.327	0.340	1	0.560
	Sex Ratio * Time of Day		0.208	1	0.649	0.139	1	0.711
	Environmental Complexity * Time of Day		0.328	1	0.567	0.132	1	0.717
Mating Effort[1]	Sex Ratio		0.529	1	0.467	0.405	1	0.525
	Environmental Complexity		0.868	1	0.352	0.013	1	0.911
	Time of Day		3.462	1	0.063	2.510	1	0.113
	Trial Day		2.996	3	0.392	0.560	2	0.745
	Average Female Age		**9.019**	**1**	**0.003**	**11.660**	**1**	**<0.001**
	Sex Ratio * Environmental Complexity		0.000	1	0.996	0.428	1	0.513
	Sex Ratio * Time of Day		0.408	1	0.523	0.037	1	0.848
	Environmental Complexity * Time of Day		2.751	1	0.097	1.062	1	0.303
Mating Skew[1,2]	*Even*	Environmental Complexity	0.062	1	0.803	*NA*	*NA*	*NA*

	Sex Ratio	Time of Day	0.369	1	0.544			
		Trial Day	2.025	3	0.567			
		Environmental Complexity * Time of Day	0.262	1	0.609			
	Female biased Sex Ratio	Environmental Complexity	0.018	1	0.892	*NA*	*NA*	*NA*
		Time of Day	0.857	1	0.355			
		Trial Day	1.220	3	0.748			
		Environmental Complexity * Time of Day	0.774	1	0.379			
Courting Count[1]	Sex Ratio		0.211	1	0.646	0.000	1	0.996
	Environmental Complexity		0.847	1	0.357	1.206	1	0.272
	Time of Day		0.125	1	0.724	0.099	1	0.754
	Trial Day		**53.177**	**3**	**<0.001**	0.065	2	0.968
	Sex Ratio * Environmental Complexity		1.347	1	0.246	0.216	1	0.642
	Sex Ratio * Time of Day		2.050	1	0.152	1.060	1	0.303
	Environmental Complexity * Time of Day		1.704	1	0.192	0.497	1	0.481

3.4.2 Intrasexual Behaviours

Male crowing activity significantly declined across trial days ($\chi^2_3 = 17.493$, $p < 0.001$). There was a significant interaction between sex ratio and time of day, where males crowed less often in the morning in the 'female biased' sex ratio (sex ratio * time of day: $\chi^2_1 = 10.458$, $p < 0.001$; post-hoc comparison of time of day in the 'female biased' sex ratio: $t = 4.145$, d.f. = 208, adjusted $p < 0.001$) but not in the 'even' sex ratio ($t = -0.539$, d.f. = 208, adjusted $p = 0.949$; **Figure 3.2**). When trial day 1 was excluded from analyses, time of day was the only significant predictor of crowing ($\chi^2_1 = 5.968$, $p = 0.015$). There was no effect of environmental complexity on crowing activity in analyses both including and excluding trial day 1 (see **Table 3.2**). When 'even' and 'female biased' flocks were considered separately, counts of crowing were significantly predicted by dominance (Elo) rank in both sex ratios (see B.1 Supplementary Results).

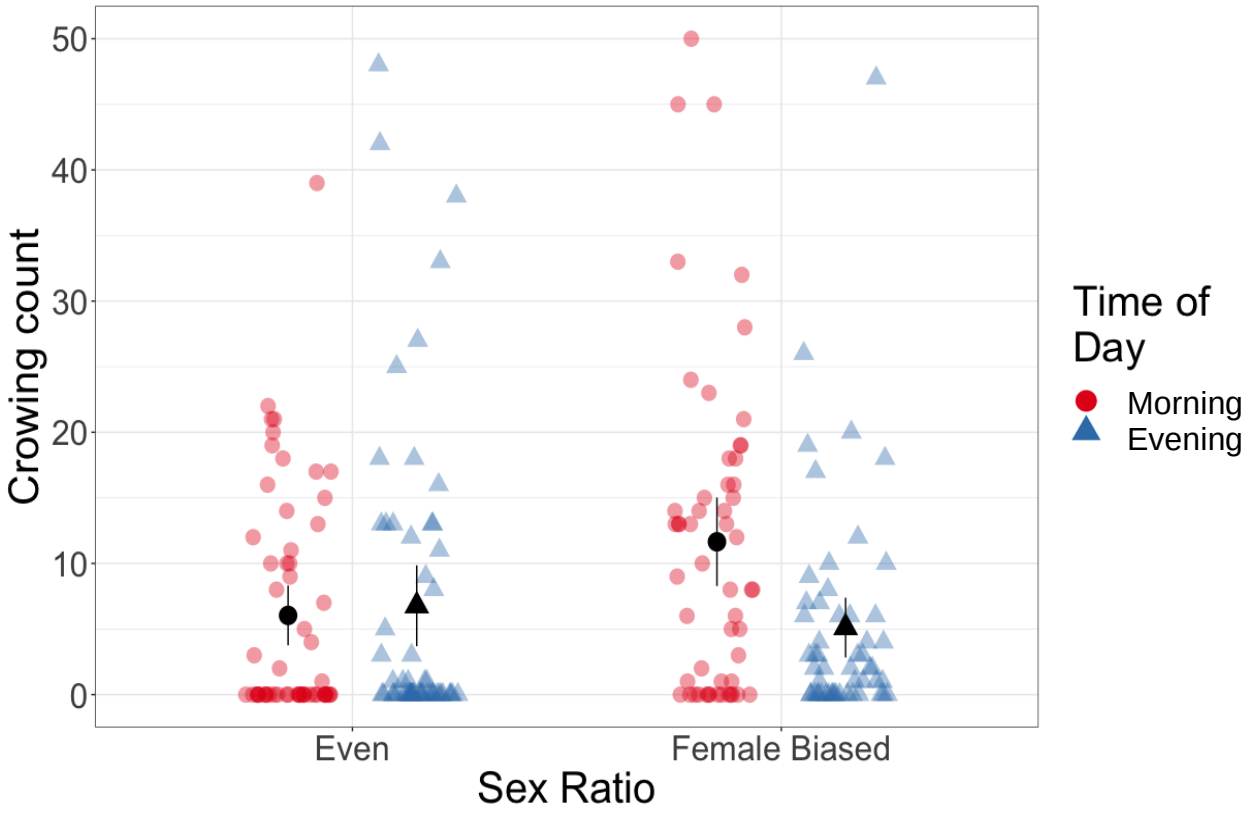


Figure 3.2: Counts of crowing within flocks of different sex ratios ('even' *vs* 'female biased') across time of day (morning *vs* evening). Individual coloured points indicate counts of crowing for individual males in the morning (red circles) and evening (blue triangles) for 5 'female biased' and 7 'even' sex ratio trials. Black points denote mean values ±95% CI.

Males performed significantly fewer wing flaps across trial days ($\chi^2_3 = 85.256$, $p < 0.001$) and counts of wing flaps depended on the interaction between time of day and sex ratio ($\chi^2_1 = 4.662$, $p = 0.031$; **Figure 3.3**). In contrast to crowing activity, however, this interaction effect was driven by an increase in wing flaps in the evening for the 'even' sex ratio (post-hoc time of day comparison: $t = -4.127$, d.f. = 208, adjusted $p < 0.001$) but not the 'female biased' sex ratio (post-hoc time of day comparison: $t = -1.120$, d.f. = 208, adjusted $p = 0.696$). When trial day 1 was

excluded from analyses, there was no effect of trial day on wing flap counts ($\chi^2_2 = 2.886$, $p = 0.236$; **Table 3.2**). Additionally, the interaction between time of day and sex ratio was reduced to a statistical trend ($\chi^2_1 = 3.134$, $p = 0.077$). As post-hoc analysis revealed a significant increase of wing flaps in the evening in the 'even' sex ratio ($t = -2.701$, d.f. = 208, adjusted $p = 0.038$), the loss of this interaction effect is presumably driven by a lack of statistical power from excluding information from trial day 1. There was no effect of environmental complexity on wing flapping activity in analyses both including and excluding trial day 1 (see **Table 3.2**).

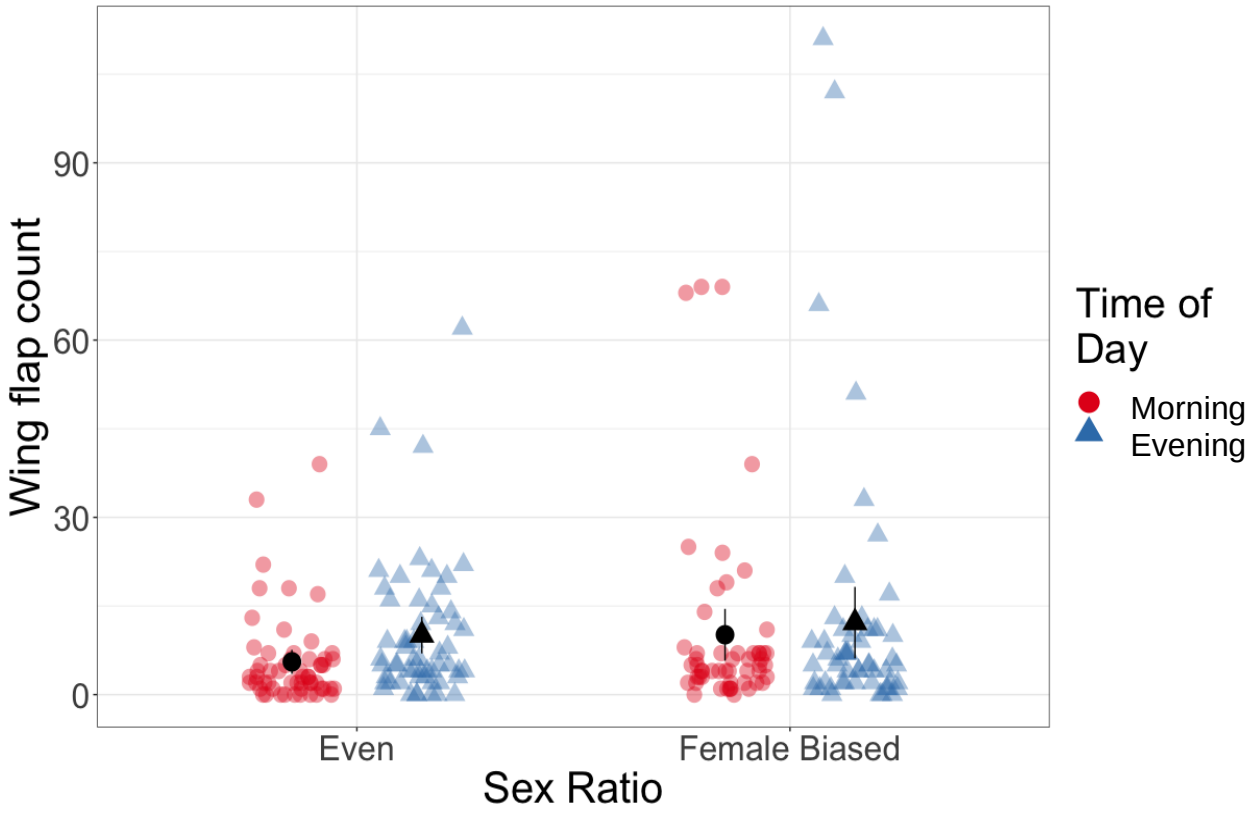


***Figure 3.3**:* Counts of wing flaps within flocks of different sex ratios ('even' *vs* 'female biased') across time of day (morning *vs* evening). Individual coloured points indicate counts of wing flapping for individual males in the morning (red circles) and evening (blue triangles) for 5 'female biased' and 7 'even' sex ratio trials. Black points denote mean values ±95% CI.

When sex ratios were considered separately, counts of wing flapping were significantly predicted by dominance rank in 'even' but not 'female biased' flocks (see **Table B.1**). Further, in 'even' flocks, when trial day 1 was excluded from analyses, a significant effect of environmental complexity was revealed ($\chi^2_1 = 6.365$, $p = 0.012$). However, there was a marginally significant interaction effect between dominance rank and environmental complexity, which may make interpreting the effect of environmental complexity more complicated ($\chi^2_2 = 4.906$, $p = 0.086$; see **Figure 3.4**). Post-hoc analysis of the interaction effect revealed that dominant males had significantly higher counts of wing flapping (*vs* lower ranked males) in 'simple' but not 'complex' environments ('simple' rank 1 *vs* 2: $t = 3.333$, d.f. = 69, adjusted $p = 0.017$; 'simple' rank 1 *vs* 3: $t = 3.652$, d.f. = 69, adjusted $p = 0.002$; 'complex' rank 1 *vs* 2: $t = 1.927$, d.f. = 69, adjusted $p = 0.395$; 'complex' rank 1 *vs* 3: $t = 3.362$, d.f. = 69, adjusted $p = 0.015$).

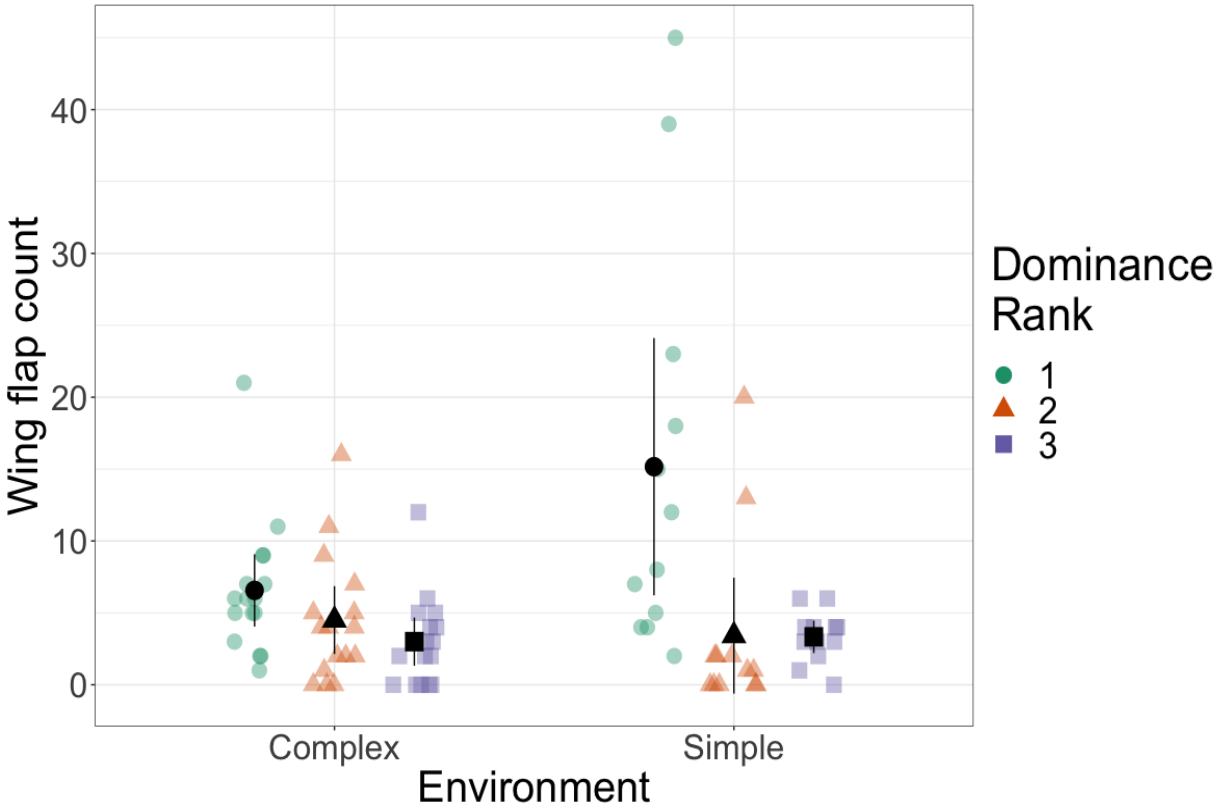


Figure 3.4: Counts of wing flaps by males of each dominance rank (1-3) across 'complex' and 'simple' environments in the 'even' sex ratio. Individual coloured points indicate counts of wing flaps for individual males each time of day across trial days for for 5 trials. Black points denote mean values ±95% CI.

Averaged summed counts of chases and lunges *per* male were higher in 'even' *vs* 'female biased' flocks when all trial days were considered ($\chi^2_1 = 4.439$, $p = 0.035$; see **Figure 3.5** and **Table 3.2**). When trial day 1 was removed, the effect of sex ratio was even stronger ($\chi^2_1 = 8.172$, $p = 0.004$; see **Table 3.2**). When all trial days were considered, the sum of chases and lunges was significantly greater when the average age of males within groups was lower, and when the average age of females within groups was higher (see **Table 3.2**). Counts of intrasexual waltzing did not significantly vary with sex ratio, environmental complexity, or over time (trial day and time of

day). This result was unchanged when intrasexual waltzing on trial day 1 was excluded from analyses (see **Table 3.2**).

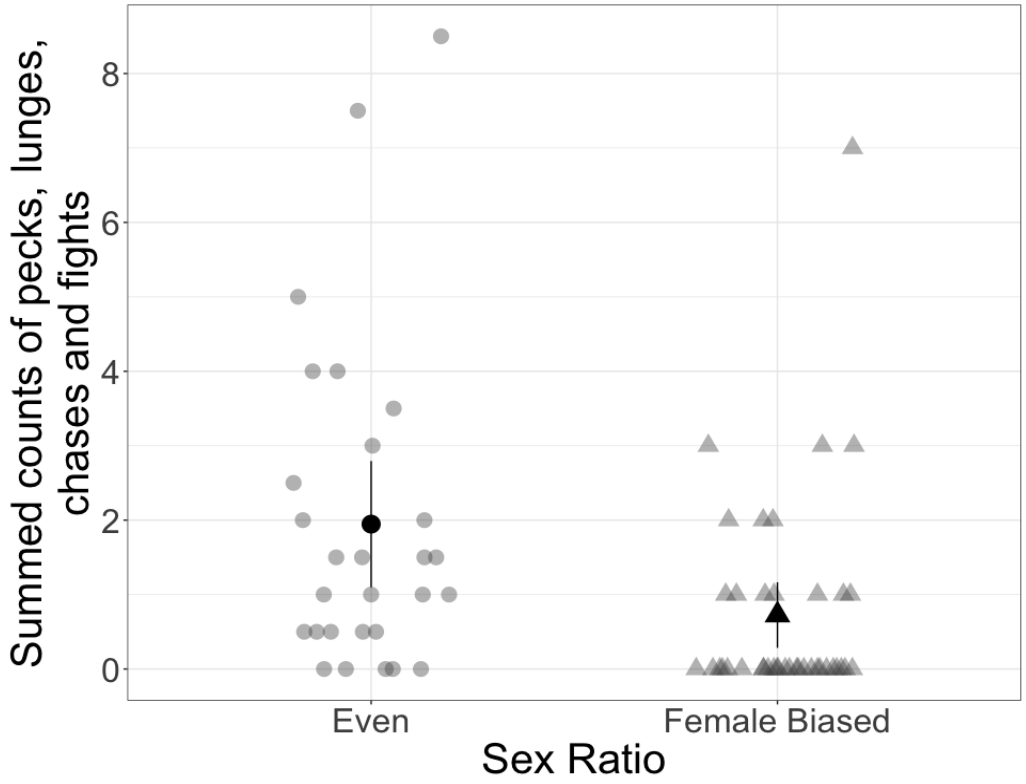


Figure 3.5*:* Summed counts of pecks, lunges, chases and fights within 'even' and 'female biased' sex ratios. Individual grey points indicate counts of summed aggressive behaviours for individual males each trial day for 5 'even' sex ratio trials (circles) and 7 'female biased sex ratio trials (triangles). Black points denote mean values ±95% CI.

Table 3.2: Male intrasexual (dominance and aggressive) behaviours. For each GLMM, a summary statistic (χ^2), degrees of freedom (df) and *p*-values are shown. Significant results ($p \leq 0.05$) are indicated in bold. [1] Indicates a model where the random effect of Observation Date explained very little variance and was removed.

Response variable	**Fixed effect/covariate**	***All days***			***Day 1 Excluded***		
		χ^2	**df**	***p***	χ^2	**df**	***p***
Crowing	Sex Ratio	0.617	1	0.432	1.112	1	0.292
	Environmental Complexity	1.331	1	0.249	1.553	1	0.213
	Time of Day	0.051	1	0.821	**5.968**	**1**	**0.015**
	Trial Day	**17.493**	**3**	**<0.001**	3.599	2	0.165
	Sex Ratio * Environmental Complexity	0.177	1	0.674	1.992	1	0.158
	Sex Ratio * Time of Day	**10.458**	**1**	**0.001**	1.927	1	0.165
	Environmental Complexity * Time of Day	1.491	1	0.222	0.638	1	0.425
Wing Flapping	Sex Ratio	1.097	1	0.295	1.071	1	0.301
	Environmental Complexity	0.421	1	0.516	2.271	1	0.132
	Time of Day	**9.098**	**1**	**0.003**	**8.034**	**1**	**0.005**
	Trial Day	**85.256**	**3**	**<0.001**	2.886	2	0.236
	Sex Ratio * Environmental Complexity	0.043	1	0.835	0.013	1	0.908
	Sex Ratio * Time of Day	**4.662**	**1**	**0.031**	3.134	1	0.077
	Environmental Complexity * Time of Day	0.188	1	0.665	1.007	1	0.316
Summed Lunges and Chases[1]	Sex Ratio	**4.439**	**1**	**0.035**	**8.172**	**1**	**0.004**

	Environmental Complexity	0.232	1	0.630	0.143	1	0.706
	Time of Day	0.121	1	0.728	0.197	1	0.657
	Trial Day	6.636	3	0.084	2.720	2	0.257
	Average Male Age	**8.092**	**1**	**0.004**		*NA*	
	Average Female Age	**6.012**	**1**	**0.014**		*NA*	
	Sex Ratio * Environmental Complexity	3.194	1	0.074	2.727	1	0.099
	Sex Ratio * Time of Day	3.753	1	0.053	2.277	1	0.131
	Environmental Complexity * Time of Day	1.430	1	0.232	0.602	1	0.438
Waltzing	Sex Ratio	0.279	1	0.597	1.038	1	0.308
	Environmental Complexity	0.930	1	0.335	0.990	1	0.320
	Time of Day	0.687	1	0.407	2.113	1	0.146
	Trial Day	2.951	3	0.399	1.559	2	0.459
	Sex Ratio * Environmental Complexity	1.709	1	0.191	0.600	1	0.439
	Sex Ratio * Time of Day	0.145	1	0.704	1.656	1	0.198
	Environmental Complexity * Time of Day	0.456	1	0.450	1.342	1	0.247

3.4.3 Space Use

Prior to the introduction of males into pen (day 0), individual females were in the central part of the floor of pens in 38.3 ± 0.02% of scans across sex ratios (see **Figure B.3**). The addition of males into pens on trial day 1 corresponded with females reducing the time they spent in the central areas of pens by more than half (17.8 ± 0.02%). However, the proportion of scans in which females were seen in the central areas of pens significantly increased over trial days ($\chi^2_3 = 74.109$, $p < 0.001$; see **Figure B.3**). As such, by trial day 4, females were seen in the central areas of pens in similar proportions (36.7 ± 0.02%) to those observed for day 0. When trial day 1 was excluded from analyses, the proportion of time females spent in the central areas of pens still showed a significant increase across trial days 2-4 ($\chi^2_2 = 13.987$, $p = 0.001$). There was no effect of environmental complexity on the proportion of time females spent in the central areas of pens in analyses both including and excluding trial day 1 (see **Table 3.3**).

Table 3.3: Female space use. For each GLMM, a summary statistic (χ^2), degrees of freedom (df) and *p*-values are shown. Significant results ($p \leq 0.05$) are indicated in bold. [1] Indicates a model where the random effect of Observation Date explained very little variance and was removed.

Response variable	Fixed effect/covariate	*All days*			*Day 1 Excluded*		
		χ^2	df	*p*	χ^2	df	*p*
Proportion of time in the central part of the floor of pens[1]	Sex Ratio	0.990	1	0.320	1.039	1	0.308
	Environmental Complexity	0.141	1	0.708	0.870	1	0.351
	Time of Day	0.343	1	0.558	1.332	1	0.248
	Trial Day	**74.108**	**3**	**<0.001**	**13.987**	**2**	**<0.001**
	Sex Ratio * Environmental Complexity	2.017	1	0.156	0.747	1	0.387
	Sex Ratio * Time of Day	0.203	1	0.653	0.204	1	0.652
	Environmental Complexity * Time of Day	2.764	1	0.096	0.149	1	0.700

3.5 Discussion

In this study, we investigated the individual and combined effects of sex ratio and environmental complexity on inter- and intrasexual behaviours in red junglefowl. Further, we examined temporal patterns in sexual behaviours and whether these varied as a result of sex ratio and environmental complexity. Sexual behaviours across flocks did not vary with sex ratio or environmental complexity, though courtship declined in frequency across successive trial days. Additionally, across trial days females spent progressively more time in the central floor of pens. For both dominance behaviours, there was a significant interaction effect between sex ratio and time of day.

Specifically, in ‘even’ flocks, wing flapping (but not crowing) increased during the evening whereas in ‘female biased’ flocks, crowing (but not wing flapping) increased in the morning. An increase in summed chases and lunges was found in ‘even’ sex ratios, but there was no effect of environmental complexity or trial day across flocks. There was no support for the predicted interaction between sex ratio and environmental complexity – predicted to be driven by a greater influence of a ‘complex’ environment in the ‘even’ sex ratio – in this study.

In this study, we predicted that the intensity of sexual behaviours would increase in the ‘even’ sex ratio as males should invest relatively more into accessing increasingly limited mating opportunities (Weir, Grant *et al.* 2011). However, we found no significant difference in counts of courting and mating between sex ratios. Counts of courtship may have remained unchanged in ‘even’ flocks if increases in intrasexual aggression (observed in this sex ratio) constrained levels of intersexual waltzing, for example due to time or energetic constraints (Clark and Grant 2010). However, no correlation between courtship and aggression was found (Spearman’s *rho* = 0.121, *p* = 0.252) suggesting no such trade-off in male reproductive strategies. Aggressive interference of intersexual behaviours by rival males may instead explain the low variance in both courtship and mating counts across sex ratios in this study (Jirotkul 1999). While interruptions to courtship were not measured, the number of matings interrupted by rival males more than tripled in ‘even’ (16.7 ± 3% of matings interrupted) *vs* ‘female biased’ (5.8 ± 3% of matings interrupted) flocks. Alternatively, instances of courtship and mating may not have increased in ‘even’ flocks if a reduced encounter rate between males and (fewer) females prevented this (Jirotkul 1999). Measures of courtship interruptions and encounter rates in future studies may be useful for elucidating the absence of an effect of sex ratio on these intersexual behaviours.

Male mating effort (i.e. the proportion of unsolicited matings) was predicted to be higher in 'even' flocks if females increase mating resistance in response to increased male presence (and subsequently, harassment) and/or males expend more effort in coercing resistant females to secure limited mating opportunities (Lovlie and Pizzari 2007). Despite this, male mating effort was unaffected by sex ratio in this study. The absence of this effect may be explained by the significant mating skew observed in the 'even' sex ratio. Specifically, as female fowl preferentially mate with higher-ranked males (Pizzari and Birkhead 2000), and these males monopolise a greater proportion of matings in 'even' flocks, females should not be expected to become increasingly resistant to mating. Alternatively, as no increase in mating counts occurred between sex ratios, there may have been no subsequent increase in female resistance in 'even' flocks prompting a higher mating effort. This was difficult to confirm in this study as information on female resistance and male energetic expenditure were combined into scores of mating effort. Combined scores of female resistance and male energetic expenditure have been previously used as these behaviours are presumed to be positively correlated (Lovlie and Pizzari 2007). However, disentangling the effects of female resistance and male mating effort in future studies may be useful in uncovering whether there are sex-specific responses to variations in the OSR.

Contrary to our predictions based on reports from previous studies (e.g. Benton and Evans 1998, Candolin 2004, Candolin and Salesto 2006, Hibler and Houde 2006, Candolin, Salesto *et al.* 2007, Myhre, Forsgren *et al.* 2013, Malek and Long 2019, Somparn, Damnoensakunchai *et al.* 2019, Wilgers, Colton Watts *et al.* 2022), the introduction of a 'complex' environment did not appear to reduce opportunities for sexual harassment. In a study of two-spotted gobies (*Gobiusculus flavescens*), habitat complexity reduced rates of male-female encounters, leading to less frequent courtship and aggressive courtship interruption by males (Myhre, Forsgren *et al.* 2013). In flocks

of domestic hens, the introduction of environmental complexity also led to a reduction in interaction frequency (Cornetto, Estevez *et al.* 2002), potentially as a result of individuals dispersing more evenly across pens (Leone and Estévez 2008). In this study, introducing environmental complexity did not alter patterns of space use (time females spent on the central floor of arenas). The moderate ranging behaviour of this species may have hindered the effectiveness of environmental complexity in reducing male-female encounter rates (and subsequently reducing the occurrence and intensity of sexual behaviours) in this study. Indeed the natural home range size of red junglefowl (1 ha *per* adult bird; Collias and Collias 1967) far exceeds the size of our study pens (21.45m^2) and territory sizes reported in commercially-housed domestic fowl (259m^2 within 1170m^2 pens). Further work should test whether the extent to which environmental complexity limits encounter rates depends on the size of the ranging area available.

Dominance behaviours (crowing and wing flapping) varied depending on the combination of sex ratio and time of day in this study. Males crowed relatively more often in the morning (*vs* evening) in 'female biased' flocks, but not in 'even' flocks. Crowing may function in the maintenance of dominance relationships and was significantly predicted by social rank in both sex ratios (Fessler, Zuk *et al.* 2001). In wild populations, junglefowl crowing activity peaks in the morning, with a relatively smaller peak in the evening (Collias and Collias 1967). The fact that crowing activity did not peak in the morning of the 'even' sex ratio might therefore indicate the suppression of this temporal pattern in these flocks. Crowing is associated with low energetic costs and so it is unlikely males reduced morning crowing activity in the 'even' sex ratio to compensate for the energetic costs of increased aggression (Chappell, Zuk *et al.* 1995). It is possible, however, that higher levels of aggression in the 'even' sex ratio were sufficient to reinforce dominance relationships, making peaks in morning crowing activity unnecessary for this purpose (Collias and Collias 1967,

McBride, Parer *et al.* 1969). Finally, crowing may function in advertising males' spatial position (McBride, Parer *et al.* 1969) and so may have been suppressed in the 'even' sex ratio to prevent further increases in aggression.

In contrast to crowing, the dominance behaviour wing flapping showed an increase in the evenings of the 'even' sex ratio only. To our knowledge, daily patterns of wing flapping have not previously been investigated in fowl and it remains unclear whether males actively increased this behaviour during evenings in the 'even' sex ratio or suppressed it in the 'female biased' sex ratio. In fowl, the value of a mating opportunity varies within each trial day, with copulations in the evening most likely to result in fertilisation success (Gracewski and Scott 1943, Parker 1945). Social rankings – which dictate priority of access to mating opportunities – might therefore be especially significant in the evenings, resulting in the increased wing flapping seen. This evening increase in wing flapping may only be evident in the 'even' sex ratio where reproductive skew is higher and males have a greater incentive to invest in dominance-related behaviours. Future work investigating how changes in wing flapping activity may predict the stability of male dominance hierarchies or reproductive skew will be useful for understanding temporal variation in this behaviour. Further, directly contrasting patterns of crowing and wing flapping may indicate subtle differences in the roles of these dominance behaviours, which are usually considered functionally non-distinct (e.g. Zuk, Thornhill *et al.* 1990, Johnsen, Popma *et al.* 1995, Johnsen, Zuk *et al.* 2001). Additional studies considering the outcomes of these behaviours (e.g. on individuals' social rank) across sex ratios and times of day may be useful in elucidating these differences.

Within 'even' flocks, dominant males performed relatively more wing flaps than subordinate males in 'simple' but not 'complex' environments (*albeit* as indicated by a non-significant statistical trend). A previous study showed male wing flapping was unaffected after pens were

expanded by cutting holes in the wall of adjoining pens (Fessler, Zuk *et al.* 2001). Our study contradicts these previous findings and suggests that environmental complexity may modulate wing flapping by restricting males' visual contact. Indeed, whereas crowing individuals may be identified based on acoustic cues alone (Miller 1978), the sound of wing flapping appears to be fairly consistent between males (H. J. P. O personal observation) and visual contact may be required for these to convey information on dominance. In 'female biased' flocks, wing flapping predicted dominance rank across both environments. This could be explained by the presence of only two males in this sex ratio, which would remove uncertainty between males over the actor of dominance behaviours. Increased wing flapping by dominant males in 'complex' environments was not reflected in any significant change in reproductive skew (complex environments have been previously reported to lower reproductive skew in sticklebacks Candolin 2004). This may indicate that crowing (unaffected by changes in environmental complexity) was sufficient to maintain dominance hierarchies when experimental barriers were erected in 'even' flocks. Further work erecting more barriers in pens may be used to assess whether mating skew is sensitive to environmental complexity in this species.

The finding that a measure of male intrasexual aggression (summed chases and lunges) was higher in 'even' flocks is consistent with previous studies which report heightened aggression with moderate increases in OSR across species (e.g. Tejedo 1988, Enders 1993, Grant and Foam 2002, Weir, Grant *et al.* 2011, Wacker, Mobley *et al.* 2013). Whilst some change in intrasexual aggression may be attributable to changing numbers of males (which alters male-male encounter rate; e.g. Debuse, Addison *et al.* 1999), summed chases and lunges more than doubled in the 'even' sex ratio. Increased male intrasexual aggression in 'even' flocks is thus likely to, at least in part, reflect intensifying competition between males for more limited mating opportunities (Emlen and

Oring 1977). In contrast to summed chases and lunges, intrasexual waltzing did not vary across sex ratios, though this behaviour was inversely correlated to both chasing and lunging. The role of waltzing in intrasexual aggression might therefore diverge from chasing and lunging and may also be moderated by alternative external factors, such as food availability (Millman, Duncan *et al.* 2000).

Courtship and dominance behaviours declined over time in this study, though these results were specifically driven by high occurrences of respective behaviours on trial day 1. As mating rates did not also decline over time, it is unlikely that the reduction of these behaviours resulted from a lessened interest in attracting mates (courting) or maintaining social ranks in order to access mates. Instead, the decline in these behaviours may be related to social familiarity following trial day 1 reducing requirements for continued courtship and dominance interactions (Kelley, Graves *et al.* 1999, Zajitschek, Evans *et al.* 2006). Across the entire trial period (4 trial days), females increased their time spent on the central floor of pens. Although mating rates remained consistent, less courtship after trial day 1 may have lowered levels of sexual harassment, encouraging females to reduce the time spent perching and on the periphery of pens and move to more exposed areas (i.e. the central floor of pens) to resume common behaviours such as perching and preening (Keeling and Duncan 1991, McDonald, Spurgin *et al.* 2019).

There was no evidence for interacting effects of sex ratio and environmental complexity on the behaviours measured in this study. This may have been partially driven by the experimental design, if exposing groups to each environmental complexity for one day at a time was insufficient to provoke plastic adjustment of behaviours in response to the changing intensity of sexual selection (Gomes and Cardoso 2020). Indeed, this experimental design – or a low sensitivity of birds to changes in environmental complexity in this study – may have reduced the capacity of individuals

across sex ratios to respond to environmental changes, preventing an interaction between these ecological effects. Further, the sex ratios of flocks in this study were relatively similar (3 females:3 males *vs* 4:2). While changes to the sex ratio of flocks was sufficient to modulate some temporal patterns of dominance behaviours, changes to levels of sexual selection may have been insufficient in prompting distinct responses between sex ratios to changes in the environment. Future studies exposing flocks to larger enclosures, exposing each flock to only 'complex' or 'simple' environments, and comparing behaviours across a broader range of sex ratios may be better in elucidating potential interactions between ecological factors in this species. Alternatively, future studies may show a weak or absent effect of environmental complexity in concordance with our results, suggesting the benefits to red junglefowl of plastically responding to changes in this ecological factor are limited.

The addition of males into flocks altered daily patterns of female spatial use across both sex ratios. In the absence of males, females spent twice as much time (~50% of scans) in the central floor of aviaries in the evenings compared to the mornings. This is surprising, given female junglefowl tend to forage in the morning and so should be especially present on the central floor of aviaries during this time (Lovlie and Pizzari 2007). However, as fertility peaks in the evening in fowl, females may instead be selected to increase their accessibility for mating, even in the absence of males (Pizzari and Birkhead 2001). When males were present, female space use in the mornings was unchanged, but females did not spend more time on the central floor of aviaries in the evening. Previous work in fowl has shown females adjust daily patterns of mating solicitation when sexual harassment is intense, soliciting relatively more matings in the morning during periods of lower male sexual interest (Lovlie and Pizzari 2007). In this study, all groups were assembled in the evenings and females were observed in the absence of males for one trial day. Further

investigations are therefore needed to confirm whether changes in female space use are in response to male harassment, or whether these initial patterns occurred due to birds' unfamiliarity with the pen.

3.6 Conclusion

Overall, this study extends our knowledge of how intra- and intersexual behaviours in red junglefowl can be shaped by ecological and temporal factors. The influence of sex ratio in this study was confined to intrasexual behaviours and the magnitude of this effect often depended on the time of day. These results highlight the importance of considering the integrated effects of temporal and ecological factors and suggest their importance in intrasexual dynamics, including the maintenance of dominance hierarchies and competitive strategies. Weak support for an effect of environmental complexity in this study contrasts with earlier work and may suggest the importance of this effect has been previously overestimated. Further work should seek to build on this by estimating the strength of sexual selection across covarying ecological factors of sex ratio and environmental complexity, and over time. Understanding the implications of natural covariance and artificial manipulations (e.g. as applied to commercial flocks of fowl; Cornetto and Estevez 2001, Cornetto, Estevez *et al.* 2002, Odén, Gunnarsson *et al.* 2005) of these ecological factors stands to further our knowledge on the operation of sexual selection.

3.7 Appendix B: Supplementary Material for Chapter 3

B.1 Supplementary Results

Intersexual Behaviours

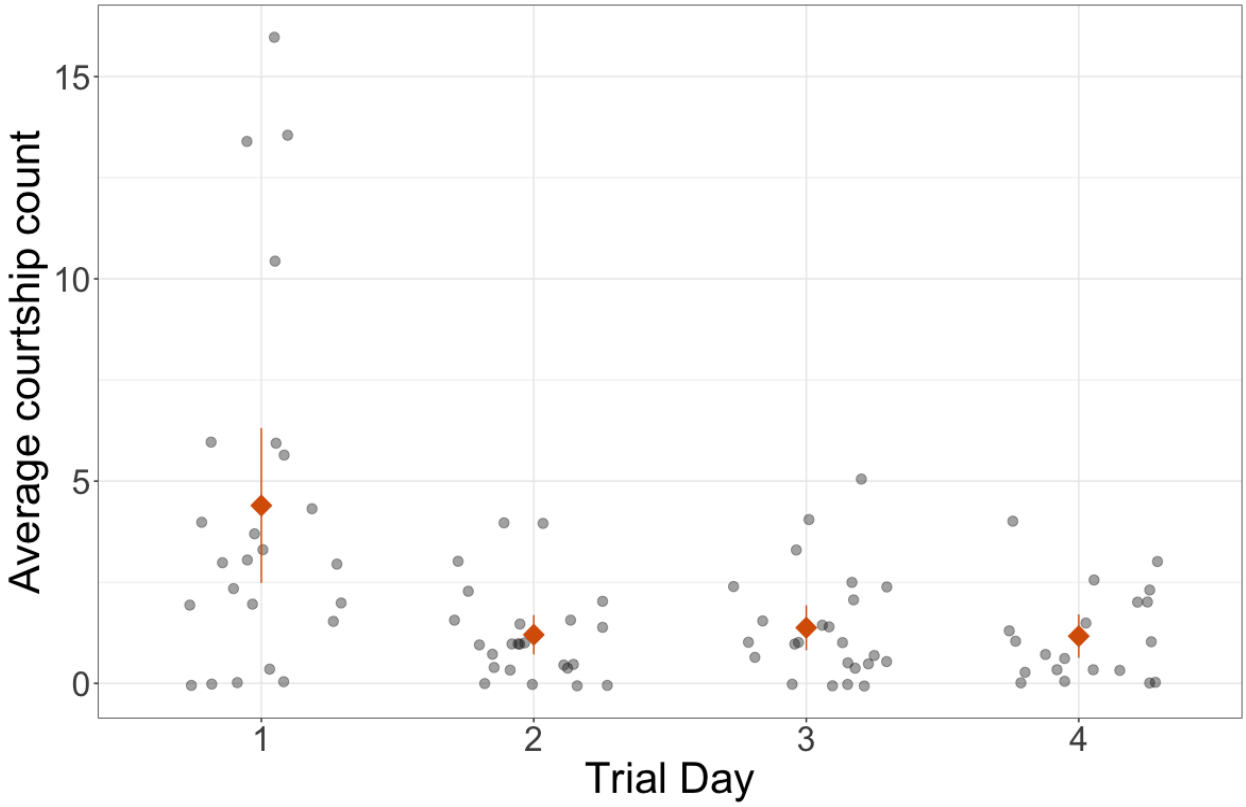


Figure B.1*:* Averaged counts of courtship by males over 4 trial days. Individual grey points indicate average counts for groups each morning and evening in 12 trials ('even' sex ratio: 5; 'female biased' sex ratio: 7). Orange diamonds denote mean values ±95% CI.

Intrasexual Behaviours

When sex ratios were considered separately, counts of crowing were significantly predicted by dominance (Elo) rank in both 'even' ($\chi^2_2 = 24.654$, $p < 0.001$) and 'female biased' ($\chi^2_1 = 10.658$, $p = 0.001$) flocks (see **Figure B.2**). Males in the 'even' sex ratio crowed less in groups where females were older on average (see **Table B.3**). When the effect of female age was controlled for, trial day was shown to be a significant predictor of crowing in the 'even' sex ratio ($\chi^2_3 = 23.224$, $p < 0.001$). There were high crowing counts on trial day 1 relative to other days (trial day 1: *vs.* trial day 2*:* $t = 4.023$, d.f. = 96, adjusted $p = 0.001$; *vs.* trial day 3*:* $t = 4.181$, d.f. = 96, adjusted $p < 0.001$; *vs.* trial day 4: $t = 2.627$, d.f. = 96, adjusted $p = 0.049$). When trial day 1 was excluded from analyses, a significant effect of time of day was revealed, with higher counts of crowing in the evening ($\chi^2_3 = 4.295$, $p = 0.038$). A high crowing count on trial day 1 in the 'even' sex ratio may therefore have obscured the effect of time of day when all trial days were considered. Within the 'female biased' sex ratio, there was a significant effect of trial day which remained when trial day 1 was excluded from analyses (see **Table B.1**). Within each sex ratio, there was no effect of environmental complexity on crowing activity both when trial day 1 was included and excluded from analyses (see **Table B.1**).

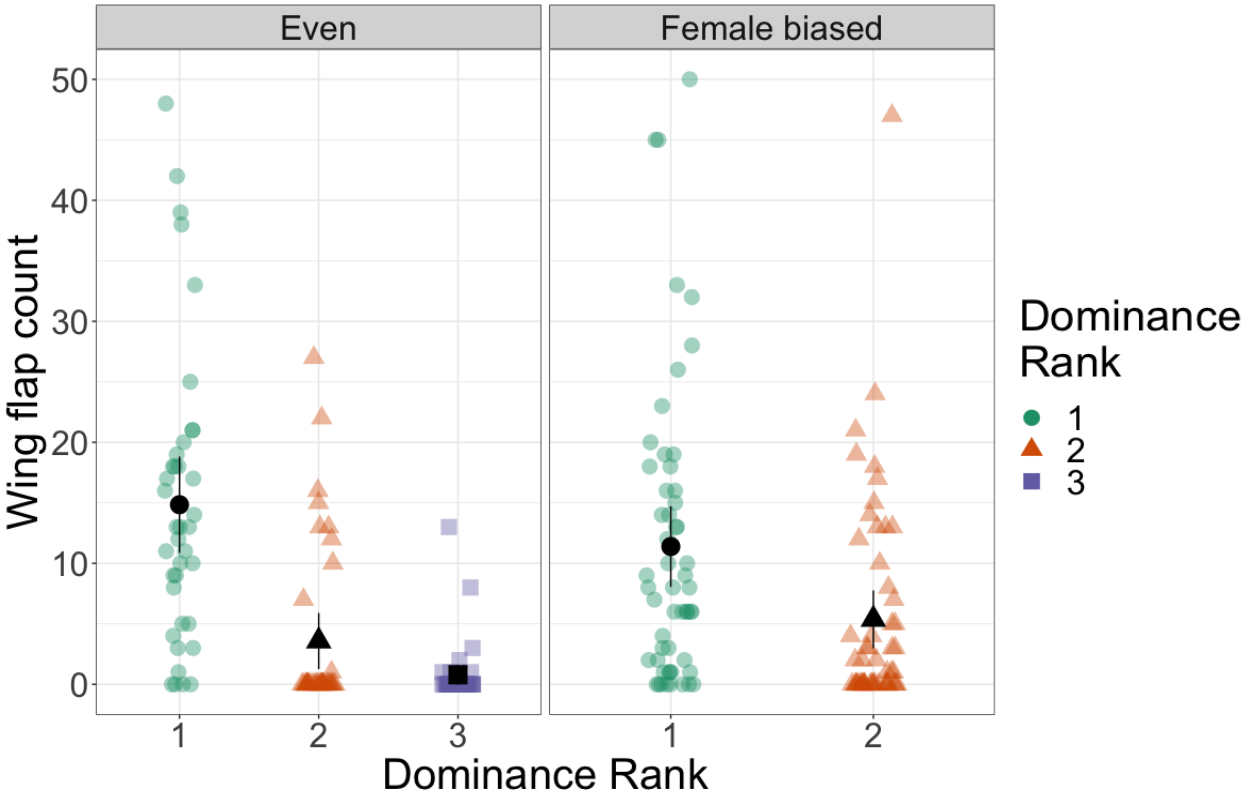


Figure B.2*:* Counts of crowing across dominance (Elo) ranks in 'even' and 'female biased' sex ratios. Individual grey points indicate crowing counts for individual males for each time of day across trial day for 12 trials ('even' sex ratio*:* 5; 'female biased' sex ratio: 7). Black points denote mean values ±95% CI.

Within the 'female biased' sex ratio, wing flapping significantly declined across trial days (χ^2_3 = 33.930, $p < 0.001$). However, post-hoc analyses indicated this result was due to especially high counts of wing flapping on trial day 1 and this finding became non-significant when trial day 1 was excluded from analyses (see **Table B.1**). There was no effect of sex ratio and environmental complexity nor time of day on wing flapping counts for analyses both including and excluding trial day 1 (see **Table B.1**).

Similar to crowing, males in the 'even' sex ratio performed fewer wing flaps in groups where females were older on average (see **Table B.1**). Additionally, older males in the 'even' sex ratio had significantly higher counts of wing flapping (see **Table B.1**). When the effects of female and male age were controlled for, there was a significant influence of trial day on counts of wing flaps ($\chi^2_3 = 33.930$, $p < 0.001$). Post-hoc analysis revealed this result was driven by high counts of wing flaps on trial day 1 (trial day 1: *vs*. trial day 2: $t = 3.652$, d.f. = 96, adjusted $p = 0.002$; *vs*. trial day 3*:* $t = 4.185$, d.f. = 96, adjusted $p < 0.001$; *vs*. trial day 4: $t = 4.771$, d.f. = 96, adjusted $p < 0.001$).

Table B.1: Male dominance behaviours of crowing and wing flapping. For each GLMM, a summary statistic (χ^2), degrees of freedom (df) and *p*-values are shown. Significant results ($p \leq 0.05$) are indicated in bold.

Response variable	**Fixed effect/covariate**		***All days***			***Day 1 Excluded***		
			χ^2	**df**	***p***	χ^2	**df**	***p***
Crowing	*Even Sex Ratio*	Environmental Complexity	0.911	1	0.340	1.732	1	0.188
		Time of Day	3.492	1	0.062	**4.295**	**1**	**0.038**
		Trial Day	**23.224**	**3**	**<0.001**	3.948	2	0.139
		Elo Rank	**24.654**	**2**	**<0.001**	**22.008**	**2**	**<0.001**
		Male Age	1.810	1	0.178		*NA*	
		Average Female Age	**6.821**	**1**	**0.009**		*NA*	
		Environmental Complexity * Time of Day	3.673	1	0.055	1.456	1	0.228
		Environmental Complexity * Elo Rank	1.207	2	0.547		*NA*	
		Elo Rank * Time of Day	**6.156**	**2**	**0.046**	0.760	2	0.760
	Female Biased Sex Ratio	Environmental Complexity	0.133	1	0.715	0.001	1	0.973
		Time of Day	**7.690**	**1**	**0.006**	**11.697**	**1**	**<0.001**
		Trial Day	3.466	3	0.325	1.913	2	0.384
		Elo Rank	**10.658**	**1**	**0.001**	**8.864**	**1**	**0.003**
		Environmental Complexity * Time of Day	0.022	1	0.882	0.008	1	0.928
		Environmental Complexity * Elo Rank	0.875	1	0.350	0.067	1	0.796
		Elo Rank * Time of Day	0.205	1	0.651	0.052	1	0.819

Wing Flapping	*Even Sex Ratio*	Environmental Complexity	0.071	1	0.791	**6.365**	**1**	**0.012**
		Time of Day	0.588	1	0.443	3.458	1	0.063
		Trial Day	**33.445**	**3**	**<0.001**	3.171	2	0.205
		Elo Rank	**9.738**	**1**	**0.002**	**7.150**	**2**	**0.028**
		Male Age	**5.489**	**1**	**0.019**		*NA*	
		Average Female Age	**4.762**	**1**	**0.029**		*NA*	
		Environmental Complexity * Time of Day	<0.001	1	0.988	1.303	1	0.254
		Environmental Complexity * Elo Rank	0.247	1	0.619	4.906	2	0.086
		Elo Rank * Time of Day	1.517	1		0.514	2	0.774
	Female Biased Sex Ratio	Environmental Complexity	1.458	1	0.227	2.104	1	0.147
		Time of Day	0.211	1	0.646	0.005	1	0.943
		Trial Day	**57.585**	**3**	**<0.001**	0.739	2	0.691
		Elo Rank	0.202	1	0.653	2.179	1	0.140
		Environmental Complexity * Time of Day	0.333	1	0.564	0.098	1	0.755
		Environmental Complexity * Elo Rank	2.462	1	0.117	1.161	1	0.281
		Elo Rank * Time of Day	2.036	1	0.154	0.461	1	0.497

Space Use

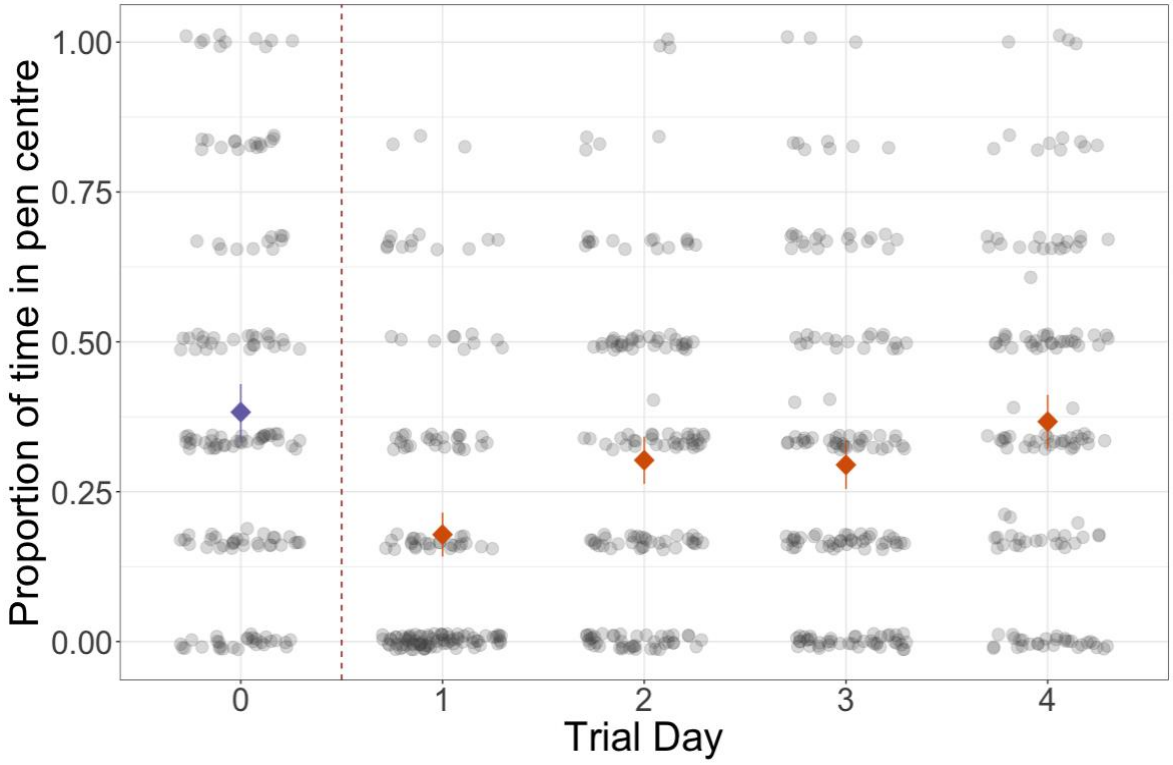


Figure B.3*:* Proportion of time spent on the central part of the pen floor by females over 5 days; 1 day preceding the introduction of males into pens (day 0), and 4 trial days. Individual grey points indicate proportional values for individual females each morning and evening within trial days for 12 trials ('even' sex ratio: 5; 'female biased' sex ratio: 7). Coloured diamonds denote mean values ±95% CI. Values for day 0 are for descriptive purposes and did not form part of the analyses.

Chapter 4: *The influence of flock composition on female-female agonistic interactions in red junglefowl*

Hannah Ogden, Albert Tremlett, Tommaso Pizzari, Jonathan Green & Eleanor Bath

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Author contributions: Tommaso Pizzari and I conceived of and designed the study. Albert Tremlett and I collected the data. I analysed the data and wrote the manuscript. The chapter was edited to incorporate comments from Tommaso Pizzari, Jonathan Green and Eleanor Bath.

4.1 Abstract

Agonistic behaviours are costly and should be strategically expressed under favourable social conditions. In species with intrasexual social hierarchies, female aggression may be limited by the presence of a highly dominant individual, or from interactions with males which are typically the dominant sex. However, the way in which dominant individuals reduce aggression among subordinates is unclear. In this study, we sought to disentangle the effects of a male or dominant female on female intrasexual aggression in red junglefowl (*Gallus gallus*) and describe how this relates to behaviours that modulate or reflect opportunities for agonistic interactions. To do this, we supplemented small flocks of four young hens with a male, an old hen or an additional young hen. Compared to flocks with all young hens, we predicted aggression would be lower in flocks containing a male, as this is the dominant sex, or old hen, as age and social status are positively correlated in females. While these predictions were initially met, aggression declined over time in

flocks with an additional young hen but increased in flocks containing an old hen and remained unchanged in flocks containing a male. Compared to young hens, the lower sociality or occupation of higher social ranks by old hens may have initially suppressed agonistic interactions among subordinates, though not effectively, as aggression increased over time. In flocks containing a male, moderate levels of sexual harassment by males towards females led to females perching more frequently and for longer than other flock types. Sustained, low levels of aggression in the presence of a male may therefore have resulted from a prolonged period of hierarchy establishment as females are less likely to (agonistically) interact upon perches. Finally, across flock types, female preening activity increased following peaks in aggression and may serve as a useful indicator of levels of aggression and associated stress within flocks. Overall, this study highlights how the age- and sex-composition of the social environment may differentially influence agonistic behaviours across different temporal scales, with implications for decision making, behavioural plasticity and sexual conflict.

4.2 Introduction

Agonistic interactions, defined broadly as aggression and related behaviours between individuals that arise through conflict (Pandolfi, Scaia *et al.* 2021), are prevalent across taxa, and occur in a variety of contexts wherever there is competition for limited resources. Within sexes, agonistic interactions may reflect competition over mating opportunities, with sexual selection favouring investment into agonistic behaviours when this improves reproductive success (Darwin 1871). In species with conventional sex roles, male reproductive rates are typically constrained by the availability of receptive females and can lead to intense and aggressive competition between males for mates (Pandolfi, Scaia *et al.* 2021). While competition between females over access to males can occur (Kvarnemo, Forsgren *et al.* 1995, Whiteman and Côté 2003, Stockley and Bro-Jørgensen 2011), female reproductive rates are more often constrained by the availability of resources associated with offspring production and survival (Fitzpatrick, Berglund *et al.* 1995). When female investment into competition directly trades off with offspring care (Rosvall 2011, Cain and Ketterson 2013), the benefits of aggression may less often outweigh the costs, compared to males. As such, females may generally engage in lower-risk behaviours and/or strategically display aggression when it is most beneficial (Stockley and Campbell 2013). For example, females may become more aggressive during periods of greater reproductive investment, such as pregnancy and lactation (Ostfeld 1985) or while guarding dependent offspring from infanticide (Walter and Trillmich 1994). Altogether, females may be expected to show more plasticity in the expression of agonistic behaviours, compared to males.

As agonistic interactions have consequences for both the agonist and competitors, the social environment should influence the costs, benefits and, ultimately, the expression of competitive

behaviours between females. For example, when the operational sex ratio is female biased or population density is high, females may benefit relatively more from agonistic interactions when this allows (a proportion of) limited resources, such as food or oviposition sites, to be monopolised (Borg, Forsgren *et al.* 2002, Rosvall 2008, Pröhl, Scherm *et al.* 2019). Additionally, female aggression may increase when this sex shows higher rates of dispersal than males and low relatedness between individuals reduces the cost of aggression (Johnstone and Cant 2008, Bose, Dabernig-Heinz *et al.* 2023).

Within many species, sex-specific social hierarchies function to reduce enduring aggression between individuals by dictating priority of access to contested resources based on asymmetries in individual competitive abilities (Kaufmann 1983). Once a social hierarchy is established, agonistic interactions may still arise when individuals attempt to displace those of higher ranks and more dominant individuals issue threats to deter this. For example, hierarchies may show altered agonistic dynamics if subordinates reduce aggression to avoid punishment by dominants (Desjardins, Hofmann *et al.* 2012, Curley 2016). Moreover, agonistic interactions may occur in series, where aggression by a dominant towards a subordinate encourages the recipient to be aggressive to a third individual who is lower ranked than the first subordinate. As aggression is often most common between closely matched competitors, groups composed of individuals distinct in their competitive abilities may show lower levels of agonistic interactions (Vaughn and Waters 1981, Dehnen, Papageorgiou *et al.* 2022). Altogether, the presence of a highly aggressive, dominant individual, or individuals with disparate competitive abilities, are expected to influence patterns of agonistic interactions within a group. However, the majority of these predictions are informed by research on male social hierarchies (Desjardins, Hofmann *et al.* 2012, Curley 2016, Dehnen, Papageorgiou *et al.* 2022). This may be problematic as, in contrast to males, rank

challenges within female hierarchies may be less common and females are often more reliant on social support from other group members (Chiarati, Canestrari *et al.* 2010, Clutton-Brock and Huchard 2013, Foerster, Franz *et al.* 2016). Further studies are therefore required to confirm the drivers of female agonistic interactions within groups.

Agonistic interactions within female social hierarchies are not independent of the opposite sex. Indeed, direct and indirect interference by males on aggression within females is possible, as males are typically the dominant sex across species (Kappeler, Huchard *et al.* 2022). For example, when males benefit relatively more from polygyny than females, sexual conflict over optimal mating systems should arise and males may actively intervene in female contests to ensure the stability of a breeding group (Davies 1986, Ren, Yan *et al.* 1991, Watts 1992, Walter and Trillmich 1994, Schradin and Lamprecht 2000, Kahlenberg, Thompson *et al.* 2008). Alternatively, the presence of a male can reduce female intrasexual aggression indirectly if females curtail agonistic interactions in response to sexual harassment (Valero, Hudson *et al.* 2005). Research considering the modifiers of female-female agonistic behaviours should thus incorporate the actions of the opposite sex, in addition to the structure of the intrasexual hierarchy.

The goal of this study is to examine the influence of flock composition on female-female agonistic behaviours in red junglefowl (*Gallus gallus*). Red junglefowl are the ancestral species to domestic fowl and show comparable social organisation, including sex-structured dominance hierarchies, with males socially dominant over females (Masure and Allee 1934, Collias and Collias 1996). Within sexes, age is an additional predictor of dominance and, in females, older hens tend to be socially dominant over younger hens (McDonald, Spurgin *et al.* 2019). Aggression between female fowl has been shown to decline in the presence of an 'alpha' (dominant) hen as this restricts subordinates' access to a defendable resource (Lamprecht and Bshary 1994). Further, female fowl

are less aggressive in the presence of a male which may be due to sexual stimulation and/or harassment suppressing hens' aggressive tendencies (Lamprecht and Bshary 1994, Odén, Vestergaard *et al.* 1999, Odén, Gunnarsson *et al.* 2005). In response to intrasexual aggression and sexual harassment, female fowl have been shown to alter their behaviours, including more frequent perching (Hughes, Carmichael *et al.* 1997, Carleial, McDonald *et al.* 2019). Unlike domestic fowl, red junglefowl have not undergone artificial selection and so retain distinct reproductive seasons. Studies on domestic fowl (Lamprecht and Bshary 1994, Odén, Vestergaard *et al.* 1999, Odén, Gunnarsson *et al.* 2005) and some other species (Davies 1986, Ren, Yan *et al.* 1991, Watts 1992, Walter and Trillmich 1994, Schradin and Lamprecht 2000, Kahlenberg, Thompson *et al.* 2008, Desjardins, Hofmann *et al.* 2012) necessarily investigate the influence of the social environment on breeding females, where energetic investment into offspring production/care may alter payoffs for agonistic interactions. Studies with red junglefowl outside of the breeding season can therefore contribute to a more complete understanding on the influence of the social environment by indicating whether predicted patterns of agonistic interactions are consistent for non-reproducing females.

In this study, we tested the influence of flock composition on female-female agonistic behaviours in red junglefowl by supplementing small flocks of four young hens with either a male, an old hen or an additional young hen. We predicted that there would be less aggression among subordinate hens in flocks supplemented with a male, due to sexual harassment or active intervention, or an old female, due to strictly enforced social ranks. Alternatively, across flock types, we predicted less aggression would occur in groups with steeper social hierarchies, as subordinates should be less likely to challenge dominants when individuals are more distinct in their competitive abilities.

Finally, we predicted that increased social familiarity between birds and, in flocks containing a male, waning interest in sexually novel females, would lead to a temporal decline in aggression.

4.3 Methods

4.3.1 Experimental Overview

We conducted our study on a captive population of red junglefowl at the John Krebs Field Station of the University of Oxford in Wytham, UK. Observations took place outside of the breeding season (typically spanning late spring to early autumn), between November 2021 and January 2022 (Year 1) and November 2022 (Year 2). Groups of four 1- year old females (hereafter 'core groups') were combined with one additional bird that was either:

1. A (1-year old) male; creating a 'male' flock
2. An 'old' (5-year old) female; creating an 'old' flock
3. A 'young' (1-year old) female; creating a 'young' flock

This created three flock types across which social structure and agonistic interactions could be compared. As differential familiarity with a site can influence the outcome of agonistic interactions and social rank, the fifth additional (hereafter 'supplemented') individual (i.e. a male, young hen or old hen, hereafter) was placed into the experimental pen with four young hens at least 48 hours before trials commenced (Maynard Smith 1979). On the first day of a trial, these four females were removed and replaced with the core group of females, creating the experimental flocks. This process allowed the supplemented individual to be more familiar with the experimental pen while preventing this individual from being socially isolated.

Flocks were observed in pens of 3.3 x 3.25 metres with two perches and *ad libitum* food and water. Behavioural observations commenced on Day 1 with the introduction of flocks into experimental arenas and ended on Day 6. Two 30-minute behavioural observations at 90-minute intervals were conducted each morning (excluding Day 1 when observations began in the afternoon) and each afternoon (excluding Day 6 when observations ended after the morning). Morning observations began on average 50 minutes after sunrise (range: 08:18 GMT – 09:06 GMT) and afternoon observations ended on average 41 minutes before sunset (range: 11:37 GMT – 13:15 GMT). Observers (H. J. P. O and A. T) collected data for up to three experimental pens (range: 2-3) in parallel so that each morning and afternoon consisted of up to six consecutive observation sessions and lasted for 3 hours. Each observer collected data on no more than one replicate *per* flock type in a given session (i.e. if three replicates were observed simultaneously there would be one replicate per flock type). The order of observations across parallel experimental pens was randomised each morning and afternoon.

Where possible, the same core group of females was exposed to all three flock types and the order of exposure was varied (see **Figure C.1** in Appendix C). As increasing familiarity of flock members may reduce levels of aggression (Craig, Biswas *et al.* 1969, D'Eath and Keeling 2003), the cumulative days that a core group had been kept together and exposed to different flock types was recorded. Due to restricted numbers of experimental birds, supplemented individuals were re-used across trials (3 males across 8 replicates; 4 old females across 9 replicates; and 4 young females across 8 replicates) and 23 young females were re-used up to 4 (average 2.17) times to create 10 distinct core groups.

4.3.2 Data Collection

To test how flock composition influenced levels of agonistic interactions among females, *ad libitum* sampling was used to record all avoidance and aggressive interactions (pecks, lunges, chases, displays and fights) between females. Vircon bands on birds' tarsi containing unique identifiers were used to record the aggressor (initiator) and target (recipient) for each interaction. Behaviours were identified using an ethogram (see **Table C.1**). Comparisons of behavioural data collected by H. J. P. O and A. T showed good interrater reliability ($\kappa = 0.82$).

In flocks containing a male, courtship and mating behaviours were recorded to provide a descriptive measure of sexual harassment of females as this was predicted to influence female-female agonistic interactions. Courtship in this species primarily consists of 'waltzing', where males extend and flutter their outer-facing wing whilst approaching a female from the side, often passing directly in front of the recipient female (Kruijt 1964). Courtship occurs regularly even outside of the breeding season (average 57.25 ± 11.56 counts of courtship within trials across days) and declined over successive trial days in this study (GLMM: $\chi^2_5 = 20.887$; $p < 0.001$). Mating (which is not necessarily preceded by courtship displays) was recorded when a male mounted a female with observed cloacal contact or when the male's train was lowered over the female's cloaca. In this study, mating occurred at low levels (average 8.75 ± 2.99 matings *per* trial) that remained consistent over time (GLMM: $\chi^2_5 = 6.939$; $p = 0.225$).

To understand emerging patterns of aggression, we measured feeding and preening (a self-grooming behaviour which may function to relieve stress; Kozak, Rozempolska-Rucińska *et al.* 2019) behaviours across flocks. How often each female perched, and the length of each perching occurrence were measured *ad libitum* during each observation period. Feeding activity was

recorded *ad libitum* with instances of feeding considered as distinct when individuals moved away from the feeder by at least 2 metres before eating again. Preening *per* female was recorded in 5-minute intervals with a binary measure (yes/no) indicating whether a female preened (arranged or oiled feathers with beak; Newberry, Keeling *et al.* 2007) and/or dustbathed (lay, sometimes on side, preening and occasionally kicking up or rubbing against the ground to distribute fine dirt through their feathers) within that time.

4.3.3 Inferring Dominance Hierarchies

In this study, we had an *a priori* prediction that flock type should influence female-female agonistic interactions, including aggression. As such, we avoided using measures of aggression to infer hierarchies within groups. Instead, the relative dominance of females within groups was determined based on avoidance behaviours, which are agonistic (one individual avoids another; see Appendix A) but are not necessarily overtly aggressive, interactions (Sapolsky and Ray 1989).

'Male' flocks in this study contained one fewer female than 'young' and 'old' flocks. In order to compare behaviours across flocks of equal size, dominant females in 'young' and 'old' flocks were identified. Dominant females and males (assumed to be dominant within flocks) were then excluded from analyses so that agonistic behaviours between subordinates could be compared across flock types. Within these groups, additional characteristics of dominance hierarchies (steepness and stability) were also calculated to more broadly assess how flock composition affected social structure.

All measures of hierarchies described below were calculated in R (v4.0.0) (R Core Team 2013) using the EloRating package (Neumann, Duboscq *et al.* 2011). Dominance was estimated by calculating David's scores for each individual, following de Vries, Stephens *et al.* (2006). While

both David's scores and Elo scores are reliable methods for inferring dominance hierarchies (Sánchez-Tójar, Schroeder *et al.* 2018) and led to highly similar estimates of dominance scores in this study (Spearman's *rho*= 0.894, $p < 0.001$), David's scores were used in this study as from these a further measure (hierarchy steepness) could be calculated. David's scores ($p_{i,j}$) were assigned based on individuals' success (individuals were 'successful' when avoided by another individual) relative to the success of all other individuals in the group. David's scores were normalised within groups so that social hierarchies could be compared between replicates and across flock types. Hierarchy steepness was calculated by regressing normalised David's scores against the rank order of individuals (De Vries, Stevens *et al.* 2006). This provided a steepness estimate between 0 and 1, describing a range from minimal to maximal differences in dominance from individuals next in rank.

We predicted that lower levels of aggression (expected in 'male' and 'old' flocks) would result in greater hierarchy stability, as fewer rank challenges would occur. Hierarchy stability was calculated using the modified stability index (S_t), with David's scores substituted in place of Elo scores (McDonald and Shizuka 2013). Briefly, S_t provides a measure between 0 (total instability) and 1 (total stability) of how often individuals within a hierarchy swap ranks and is typically summed to compare changes across consecutive days. Dominance hierarchies are most reliably calculated when the ratio of interactions (here, avoidances) to individuals is at least 10 (Sánchez-Tójar, Schroeder *et al.* 2018). As this ratio was <10 within some trial days (across all flock types) in our study, S_t was instead calculated by comparing changes in dominance ranks between the first (trial days 1-3) and second (trial days 4-6) half of trials.

4.3.4 Statistical Analysis

Statistical models were run in R (v 4.0.0) (R Core Team 2013). Unless otherwise specified, generalised linear mixed models (GLMMs) were used to test how changes in female behaviour varied across flock types and over time. The 'performance' package (Lüdecke, Ben-Shachar *et al.* 2021) was used to assess zero-inflation and overdispersion. Most models exhibited overdispersion (exceptions detailed below) and were therefore fitted with a negative binomial distribution using the 'glmmTMB' package (Brooks, Kristensen *et al.* 2017).

All models contained a fixed effect of Flock Type, a covariate of trial day and a two-way interaction of flock type * trial day. Despite a relatively small sample size (n = 8 'male' flocks; n = 8 'young' flocks; n = 9 'old' flocks), trial day was entered as a covariate so that regression slopes (calculated with the 'emmeans' package; Lenth, Singmann *et al.* 2019) could be used to compare temporal trends in behaviours across flocks. In addition, as many core groups were exposed to multiple flock types, all models contained a covariate of familiarity, defined as the number of days core groups had spent in flocks with a supplemented individual until the first day of a replicate. Between Years 1 and 2, experimental birds were kept in large (mixed-sex groups) of up to 86 individuals. Thus, familiarity was considered to be 0 when core groups were first re-assembled in Year 2.

Random effects of 'core group ID' and 'supplemented individual ID' were added to all models. Additionally, a random effect of 'observation block' was added as external factors (e.g. weather) may reduce behavioural variation among flocks observed in parallel. In some cases (noted below), random effects explained very little of the model variance and led to singularity effects and were therefore removed from the final model.

Model outputs were interpreted using a Type III Wald χ^2 test from the 'car' package, which tests for the presence of both main and interaction effects (Bolker, Brooks *et al.* 2009, Fox, Weisberg *et al.* 2012). When the interaction effect (flock type*trial day) was non-significant, this was removed and the model was reanalysed using a Type II Wald χ^2 test. The 'emmeans' package was used to conduct post-hoc analyses on models with a significant interaction effect (Lenth, Singmann *et al.* 2019).

Female Age and Dominance

To test whether old hens were more likely to become dominant than young hens when added to a core group, the social rank of supplemented individuals was added as an ordinal response variable to a CLM (Cumulative Link Model; run with the 'ordinal' package; Christensen 2015). No random effects could be included in the model due to a small sample size (n = 17 'old' and 'young' flocks) and low variation in the response variable. Results from this model should therefore be interpreted with caution.

To test whether top-ranking hens had higher dominance scores in 'old' *vs* 'young' flocks, the David's score of the top-ranking individual was added as a response variable in an LMM.

Aggression

Counts of aggression were entered as a response variable in a GLMM. As aggression may vary between individuals and depend on how pairs of individuals interact, aggressive behaviours were summed at the dyadic level. This meant that, for a pair of birds (e.g. A and B), summed counts of aggressive behaviours by A towards B and by B towards A were combined. As hierarchy stability did not vary significantly across flock types ($\chi^2_2 = 3.751$, $p = 0.153$), it was assumed that the

direction of aggression within dyads (i.e. the proportion of aggression initiated by the higher-ranking individual within a pair) was similar across flocks. Flock type, trial day and their interaction were included as fixed effects/covariates in the GLMM. To account for the re-use of individuals, Dyad ID was entered in the model as a random effect.

Limited maneuverability on perches may restrict opportunities for aggression (Nicol, Gregory *et al.* 1999). Differences in aggression across flock types may thus be explained by changes in perching behaviour across flock types (predicted *a priori*) rather than females being more prone to be aggressive each other. To disentangle these effects, the time in minutes that at least one bird within a dyad was perching was included as a covariate in the GLMM.

In this study we excluded dominant individuals (the top-ranking hen or male) from analyses to compare behaviours between four subordinate females across flock types. We had *a priori* predictions that old hens would obtain the top social rank but no such predictions for the social rank the supplemented young individual should obtain. As such, it was expected that the supplemented individual - that was unfamiliar to the core group - would be removed more often (as the 'dominant individual' in analyses) from 'old' *vs* 'young' flocks. In many species, including junglefowl, an unfamiliar individual introduced into a group may be involved in much of the ensuing aggression while dominance hierarchies are re-established and the social status of this newcomer is determined (Guhl and Allee 1944, Addison and Baker 1982, Thompson 1993, Cloutier and Newberry 2002, Neisen, Wechsler *et al.* 2009). Thus, to disentangle the effects of familiarity from flock type, an additional GLMM for 'old' and 'young' flocks including all 5 females was run.

Individuals were predicted to be less aggressive in flocks with steeper hierarchies, as challenges to social ranks by subordinates should be less common if individuals are distinct in their competitive abilities. To test this, an additional GLMM was run replacing the fixed effect of flock type with a covariate of hierarchy steepness.

Underlying Drivers of Aggression

Hierarchy Stability

To test how hierarchy stability varied with flock type, modified stability index (S_t) measures were converted to a binary measure (1 or <1) and entered as a response variable in a GLMM fitted with a binomial distribution. As S_t measures hierarchy stability over time, trial day (and the interaction between trial day and flock type) were excluded from the model.

Perching

Perching duration (minutes) and counts of perching by females were entered as response variables in separate GLMMs along with fixed effects/covariates of flock type, trial day and their interaction. Female ID was included in GLMMs as a random effect. Measures of perching duration contained more zeros than were predicted by the negative binomial distribution. The outcome of this model is presented in the Results, however, as applying a zero-inflated parameter further reduced the fit of the model though led to qualitatively similar results.

Feeding

The number of times each female fed was entered as the response variable in a GLMM along with fixed effects/covariates of flock type, trial day and their interaction. Female ID was added as a random effect.

Preening

The proportion of scans in which each female was observed preening *per* day was calculated. As proportional data were normally distributed, proportions were entered as the response variable in a linear mixed model (LMM) along with fixed effects/covariates of flock type, trial day and their interaction. Female ID was included in the LMM as a random effect.

Network Measures

A significant difference in aggression between 'old' and 'young' flocks was apparent despite no effect of flock type on the David's score of top-ranking hens. To understand whether this difference was due to differences in sociality between supplemented (old *vs* young) individuals, social networks were produced for each trial day for these flock types. Social networks were undirected, and edges were weighted by counts of avoidances between flock members. Node strength (calculated in the 'igraph' package; Csardi and Nepusz 2006) was used as a proxy of individual sociality and entered as the response variable in a GLMM (McDonald, Spurgin *et al.* 2019). To determine how node strength varied relative to the sociality of the flock, the GLMM was weighted by the summed node strengths within the social network and a binomial distribution was applied.

4.4 Results

4.4.1 Female Age and Dominance

In ‘old’ and ‘young’ flocks, the social rank a supplemented hen obtained within flocks was predicted by her age (CLM: z = 2.861, $p = 0.004$; **Figure 4.1a**). Old hens supplemented into core groups became dominant in 7 of 9 replicate trials. In one ‘old’ flock, the dominance rank of the supplemented (old) hen changed between the first and second half of observations. Excluding this trial did not alter the significance of these findings. Young hens supplemented into core groups became dominant in only 1 of 8 trials and occupied the lowest social rank in 5 of 8 trials. The familiarity of the core group (i.e. the number of days a core group had spent together in the presence of a supplemented individual before the current trial) did not influence the social rank supplemented hens obtained (CLM: z = 0.041, $p = 0.967$).

Top-ranking hens were invariably dominant between the first and second three-day period of observations. There was no significant difference in the dominance score of the top-ranking hen between ‘old’ and ‘young’ flocks ($\chi^2_1 = 1.163$, $p = 0.281$; **Figure 4.1b**). Additionally, the dominance score of the top-ranking hen was unaffected by the familiarity of the core group of hens ($\chi^2_1 = 0.002$, $p = 0.968$).

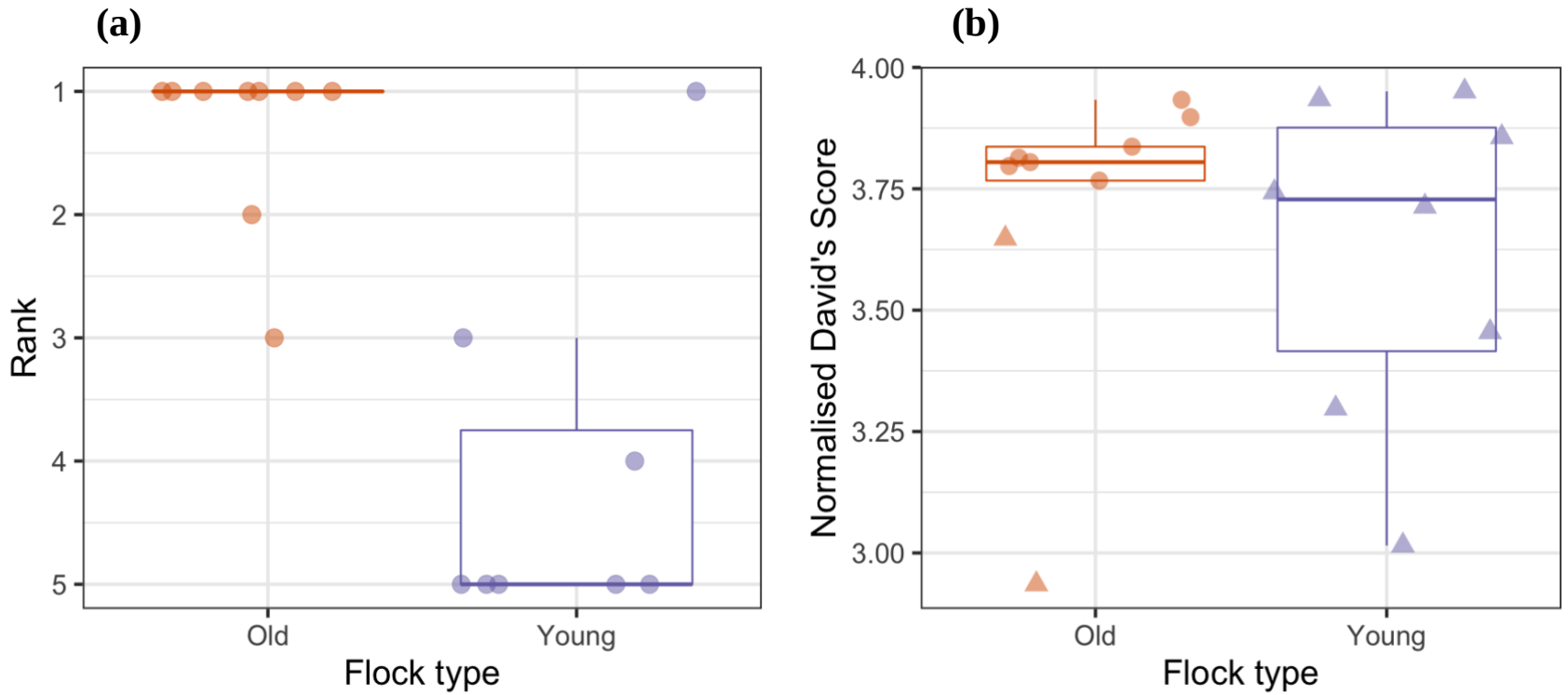


Figure 4.1: Boxplot summarising (a) the social rank of supplemented hens in 'old' and 'young' flocks; and (b) Normalised David's score of top-ranking individuals in 'old' and 'young' flocks. In (a), individual points indicate the social rank of a supplemented individual from each replicate trial. In (b) individual points indicate the Normalised David's score of the dominant individual from each replicate trial. Triangular points denote a young (1-year old) hen and circular points denote an old (5-year old hen). For both (a) and (b), boxes denote the interquartile range (IQR: Q1 – Q3), including the median (Q2; thick horizontal line). Whiskers indicate the minimum (Q1 – 1.5 * IQR) and maximum (Q3 + 1.5 * IQR) ranges of data, excluding outliers.

4.4.2 Aggression

There was a significant negative relationship between core group familiarity and aggression (χ^2_1 = 11.073, $p < 0.001$), with less aggression during trials in core groups that had been established for longer. Controlling for this effect, we found a significant interaction effect between trial day and flock type (χ^2_2 = 28.604, $p < 0.001$; **Figure 4.3**). This interaction was in part driven by counts of aggression in 'young' flocks, which were highest across flock types on trial day 1 and lowest across flock types by trial day 6 (see **Table C.2**). In contrast to the temporal decline in aggression seen in 'young' flocks (t = -4.766, d.f. = 887, adjusted $p < 0.001$), counts of aggression increased over time in 'old' flocks (t = 2.205, d.f. = 887, adjusted $p = 0.028$) while no change was seen in 'male' flocks (t = 1.132, d.f. = 887, adjusted $p = 0.258$). When aggression between all five females in 'old' and 'young' flocks was considered, a significant interaction effect between trial day and flock type remained (see **Table C.3**).

When all flocks were considered together, aggression did not depend on the steepness of hierarchies within core groups and did not vary over time (**Table 4.1**).

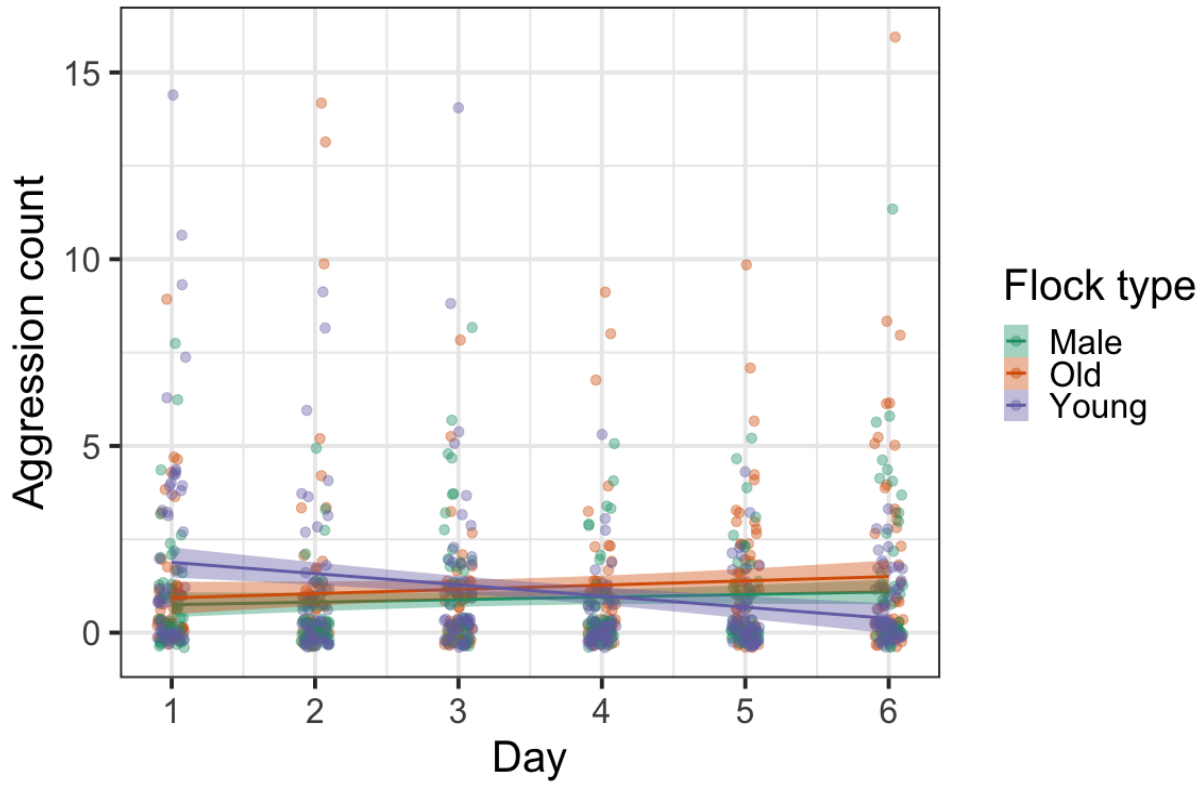


Figure 4.3: Temporal patterns of aggression in relation to flock type. Individual plots indicate counts of aggression for each dyadic combination of hens (excluding the dominant hens in flocks supplemented with an old or additional young hen) *per* day. Regression lines from a linear model with ±95% confidence intervals are indicated for each flock type.

4.4.3 Underlying Drivers of Aggression

Hierarchy Stability

The stability of hierarchies did not vary significantly across flock types ($\chi^2_2 = 0.248$, $p = 0.883$) or depend on the familiarity of hens in the core group ($\chi^2_1 = 0.540$, $p = 0.462$).

Perching

Perching duration significantly varied across flock types (χ^2_2 = 9.181, p = 0.010; see **Figure 4.4**), with hens perching around three times longer (36.24 ± 18.62 minutes) in 'male' *vs* 'old' (12.95 ± 5.30 minutes) or 'young' (9.93 ± 3.57 minutes) flocks. Perching duration did not vary across trial days or depending on the familiarity of the core group of hens (see **Table 4.1**).

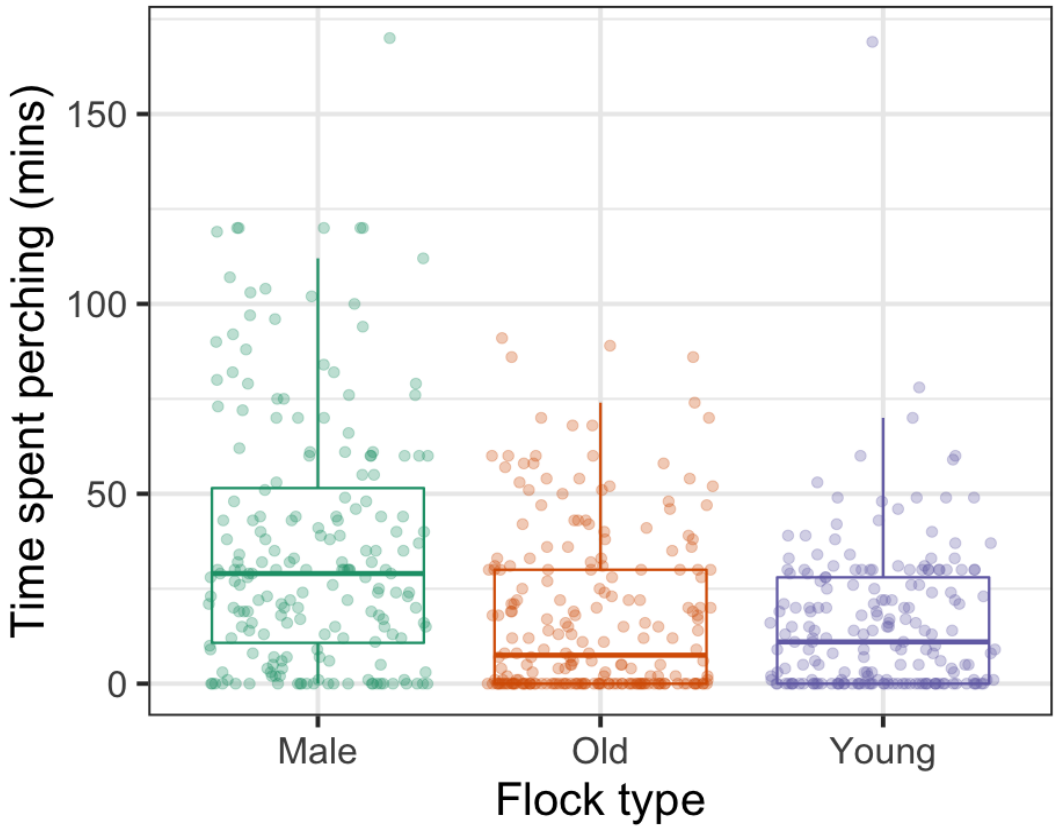


Figure 4.4: Perching duration of hens in relation to flock type. Boxes denote the interquartile range (IQR: Q1 – Q3), including the median (Q2; thick horizontal line). Whiskers indicate the minimum (Q1 – 1.5 * IQR) and maximum (Q3 + 1.5 * IQR) ranges of data, excluding outliers. Individual points indicate perching duration for individual hens.

Temporal trends of perching counts depended on flock type, resulting in a significant interaction effect ($\chi^2_2 = 7.290$, $p = 0.026$; **Figure 4.5**). This interaction was driven by a significant difference in perching counts over time between 'young' and 'old' flocks ($t = 2.690$, d.f. = 588, adjusted $p = 0.020$). Specifically, while perching counts significantly declined across days in 'young' flocks ($t = -2.892$, d.f. = 588, adjusted $p = 0.004$), no temporal change was seen in 'old' flocks ($t = 0.848$, d.f. = 588, adjusted $p = 0.397$). Perching counts in 'male' flocks did not vary across days ($t = -1.233$, d.f. = 588, adjusted $p = 0.218$), though this was not significantly different from temporal trends of perching counts in 'young' flocks ($t = 1.530$, d.f. = 588, adjusted $p = 0.277$). Counts of perching did not depend on the familiarity of hens within the core group (see **Table 4.1**).

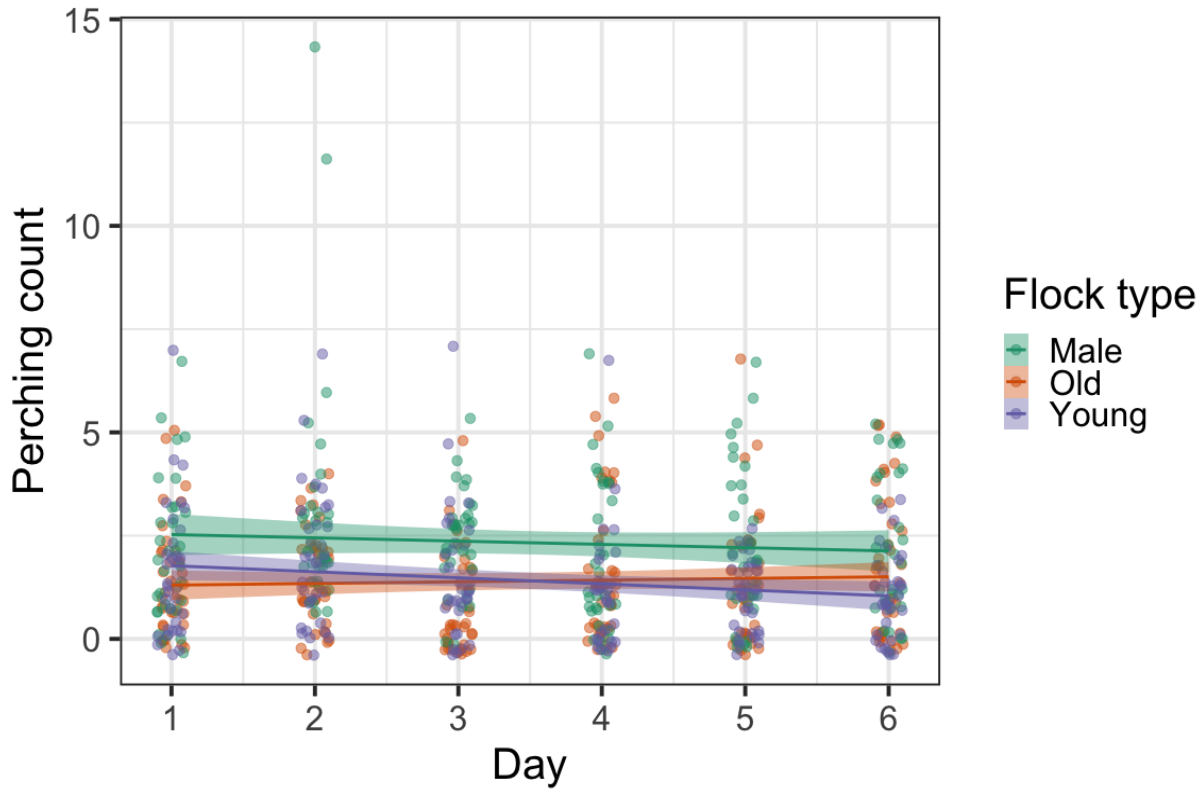


Figure 4.5: Temporal patterns of perching count in relation to flock type. Individual plots indicate counts of perching for each hen (excluding the dominant hens in flocks supplemented with an old or additional young hen) *per* day. Regression lines from a linear model with ±95% confidence intervals are indicated for each flock type.

Feeding

Feeding may leave hens vulnerable to sexual harassment or may be reduced for some individuals when this resource is guarded by a highly dominant individual. As such, female feeding counts were predicted to be lower in flocks containing a male or old hen. However, feeding counts were not significantly influenced by flock type and did not vary over time or depend on the familiarity of hens in the core group (see **Table 4.1**).

Preening

As preening may function to relieve stress, we predicted patterns of preening across flock types would be positively related to patterns of aggression. However, we found the opposite to be true. In 'young' flocks, females increased the proportion of time they spent preening across trial days (t = 5.657, d.f. = 555, adjusted $p < 0.001$). In contrast, females spent proportionally less time preening across trial days in 'old' flocks (t = -2.482, d.f. = 555, adjusted $p = 0.013$). Finally, females did not change preening behaviour across trial days in 'male' flocks (t = 1.698, d.f. = 555, adjusted p = 0.090). Overall, this led to significant interaction effect between flock type and trial day (χ^2_2 = 33.912, $p < 0.001$; see **Figure 4.6**). Preening activity did not vary with the familiarity of hens within the core group (see **Table 4.1**).

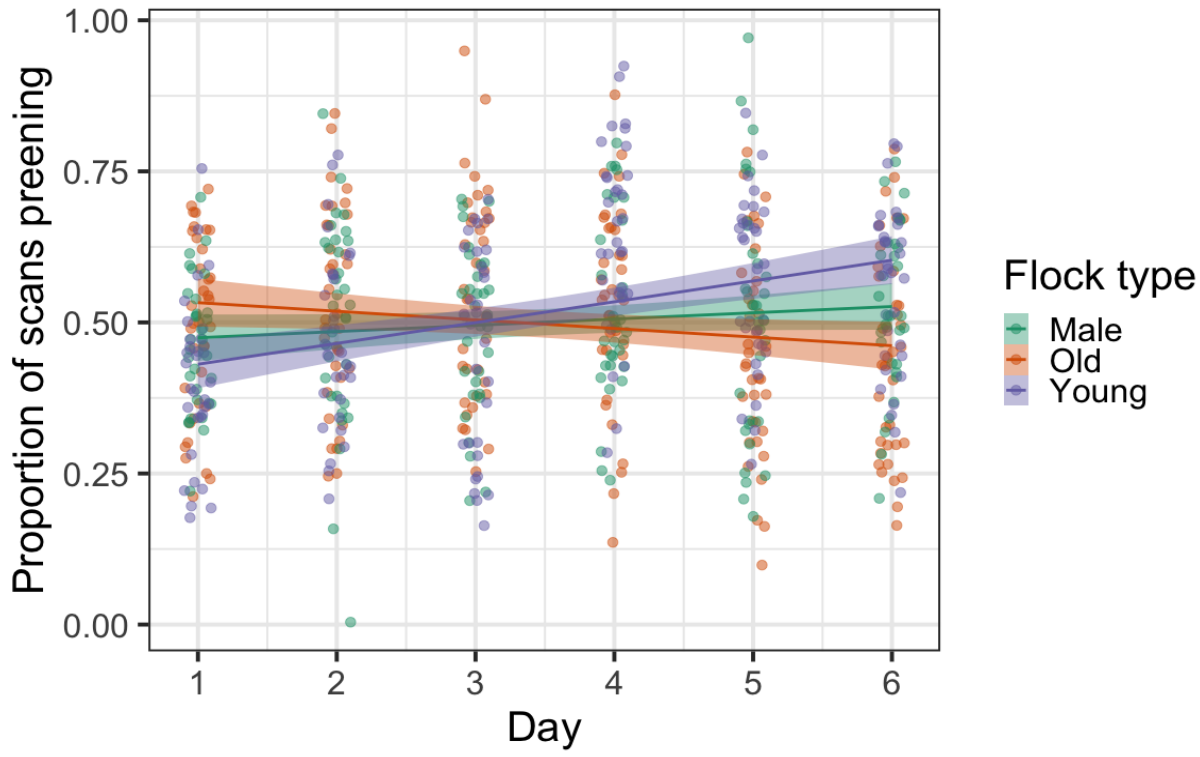


Figure 4.6: Temporal patterns of preening in hens in relation to flock type. Individual plots indicate proportions *per* hen (excluding the dominant hens in flocks supplemented with an old or additional young hen) *per* day. Regression lines from a linear model with ±95% confidence intervals are indicated for each flock type.

Table 4.1: Summarising statistical outputs for GLMMs investigating changes in female behaviour in response to changes in flock composition and hierarchy structure. For each GLMM, χ^2, degrees of freedom (df) and *p*-values are shown. Significant results ($p < 0.05$) are indicated in bold.

Response Variable	Fixed Effect/Covariate	χ^2	df	*p*
Aggression	**Flock Type**	**22.145**	**2**	**<0.001**
	Day	1.283	1	0.257
	Familiarity	**11.073**	**1**	**<0.001**
	Perching Time	0.634	1	0.426
	Flock Type * Day	**28.604**	**2**	**<0.001**
Aggression *vs* hierarchy steepness	Hierarchy Steepness	0.090	1	0.764
	Day	0.596	1	0.440
	Familiarity	**6.452**	**1**	**0.011**
	Perching Time	0.802	1	0.370
Perching Duration	**Flock Type**	**9.181**	**2**	**0.010**
	Day	0.028	1	0.868
	Familiarity	0.101	1	0.751
Perching Count	**Flock Type**	**9.810**	**2**	**0.007**
	Day	1.521	1	0.218
	Familiarity	0.066	1	0.798
	Flock Type * Day	**7.235**	**2**	**0.027**
Preening	**Flock Type**	**13.379**	**2**	**0.001**
	Day	2.884	1	0.089
	Familiarity	0.764	1	0.382
	Flock Type * Day	**33.912**	**2**	**<0.001**
Feeding	Flock Type	1.404	2	0.496
	Day	0.015	1	0.902
	Familiarity	0.163	1	0.687

4.4.4 Social Networks

The old hens that were supplemented into core groups were significantly less social (shown by a lower node strength) than additional young hens supplemented into core groups ($\chi^2_1 = 58.209$, $p < 0.001$; **Figure 4.7**). Additionally, the sociality of supplemented individuals was significantly lower when they were introduced to core groups that had been established for longer ($\chi^2_1 = 3.896$, $p = 0.048$). There was no effect of trial day on node strength ($\chi^2_1 = 1.927$, $p = 0.165$).

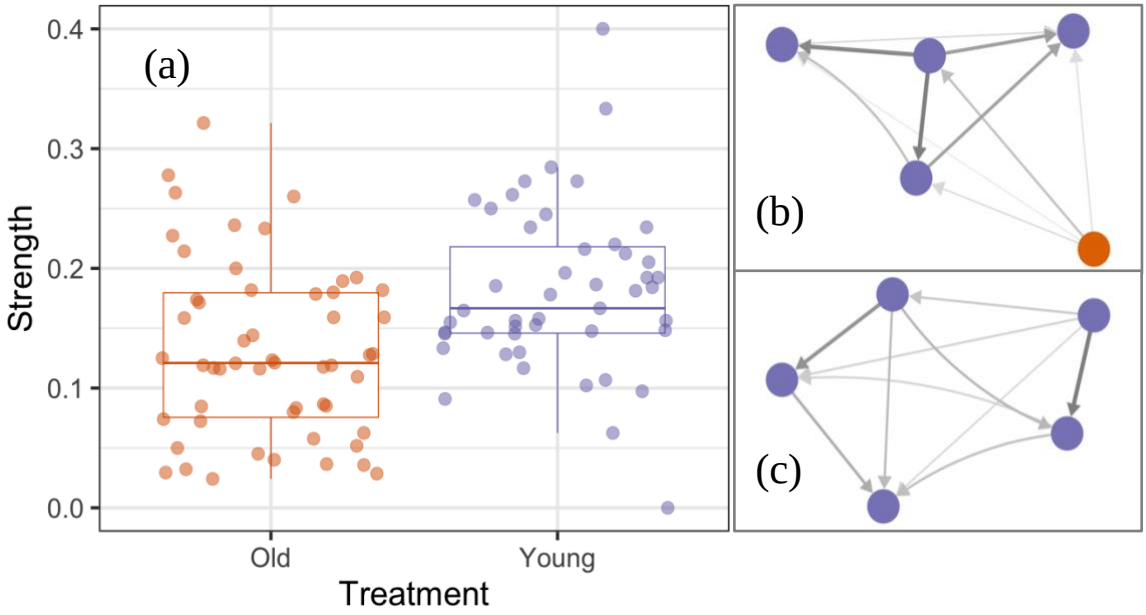


Figure 4.7: Showing (a) the sociality (node strength) of supplemented individuals in 'old' and 'young' flocks; and visual representations of social networks for (b) an 'old flock, and (c) a 'young' flock. In (a) boxes denote the interquartile range (IQR: Q1 – Q3), including the median (Q2; thick horizontal line). Whiskers indicate the minimum (Q1 – 1.5 * IQR) and maximum (Q3 + 1.5 * IQR) ranges of data, excluding outliers. Individual points indicate node strength for individual hens. In (b) and (c) nodes represent each hen within a flock (orange = old hen; purple = young hen). Network edges show the direction of avoidances (initiator to target) and are weighted by the total count of avoidances within each dyad.

4.5 Discussion

Patterns of agonistic interactions between individuals should be sensitive to aspects of the social environment, such as the presence of a dominant individual. How – and to what extent – dominant individuals shape opportunities for agonistic interactions between females, however, remains little understood. In this study, we sought to disentangle the effects of two types of dominant individual (a male or old hen) on female intrasexual aggression by supplementing flocks of four young females with a male, an old hen or an additional young hen. Overall, we found that levels of female intrasexual aggression were initially highest in 'young' flocks and declined across trial days, in contrast with aggression in 'old' and 'male' flocks. Subsequently, aggression increased across trial days in 'old' flocks but remained unchanged over time in 'male' flocks. Although supplemented hens in 'old' flocks ascended to relatively higher ranks than supplemented hens in 'young' flocks, the dominance of top-ranking hens did not vary between these two flock types. However, top-ranking hens in 'old' flocks were less social, which may have influenced patterns of agonistic interactions among the remaining flock members. Across flock types, differences in aggression between flock types were unrelated to both the stability and steepness of dominance hierarchies, both of which may be expected to mediate opportunities for aggression *via* challenges of social rank. Further, perching activity varied across flock types (with females in 'male' flocks notably perching more often and for longer) and may have altered opportunities for agonistic interactions, as aggression during perching is uncommon. However, when perching duration was controlled for, differences in aggression between flock types remained. Altogether, these results indicate that the composition of flocks alters both the opportunity and tendency for female intrasexual aggression in red junglefowl.

In contrast to temporal trends in ‘male’ flocks, levels of aggression did not remain stable over time in ‘young’ or ‘old’ flocks. However, only ‘young’ flocks showed predicted temporal declines in aggression, whereas aggression in ‘old’ flocks increased across trial days. In ‘young’ flocks, aggression likely declined as individuals became more socially familiar and established dominance hierarchies through accumulated agonistic interactions. In ‘old’ flocks, aggression may have increased if initially low levels of aggression delayed the establishment of dominance hierarchies. Indeed, though top-ranking hens did not have higher David’s scores in ‘old’ (*vs* ‘young’) flocks, supplemented hens occupied the top social rank in the majority (7 of 9) of replicate trials compared to 1 (of 8) trials in ‘young’ flocks. The presence of this dominant, unfamiliar hen may encourage short-term reductions in aggression if subordinates moderate their agonistic interactions to avoid punishment (Desjardins, Hofmann *et al.* 2012, Curley 2016). Subsequently, if infrequent aggression creates uncertainty over dominance relationships, heightened aggression may occur (e.g. as has been reported in pigs, *Sus scrofa domesticus*; Desire, Turner *et al.* 2015). However, as initial levels of aggression in ‘male’ flocks were comparably low but did not increase over time, an alternative reason for increasing aggression in ‘old’ flocks may be in how dominance hierarchies were established (Tibbetts, Pardo-Sanchez *et al.* 2022). As older female fowl generally occupy higher social ranks (McDonald, Spurgin *et al.* 2019; this study), cues of age, such as comb size (Cornwallis, Dean *et al.* 2014) may be initially used to determine dominance. Once group members become familiar – and have gained information about one another’s competitive abilities – aggression may be utilised to consolidate the order of these convention-based social hierarchies. A similar pattern has been previously shown in barnacle geese (*Branta leucopsis*), where goslings determine dominance relationships based on intrinsic attributes of body mass and size only when unfamiliar with each other (Black and Owen 1987).

Dominant individuals are often especially well-connected within social networks (Dey, Reddon *et al.* 2013, Maguire, DeAngelis *et al.* 2021) and may have a disproportionate effect on the social dynamics of the group (Watters and Sih 2005). However, in this study, old hens supplemented into flocks were notably less social (i.e. avoided and were avoided by young hens less often) than young hens supplemented into flocks. Differing sociality between old and young supplemented individuals may additionally explain the alternative temporal trends in aggression between these flock types. For example, old hens may be less effective at deterring aggression among young hens if the latter perceive punishment to be unlikely from a relatively asocial individual (Vaughn and Waters 1981, Desjardins, Hofmann *et al.* 2012, Curley 2016, Dehnen, Papageorgiou *et al.* 2022). In this study, the reduced social connectedness of older individuals may reflect increasing social selectivity and occur if accumulated social experience reduces the need to gather social information *via* agonistic interactions (Brent, Ruiz-Lambides *et al.* 2017). Alternatively, the lower sociality of old females may reflect the tendency of female junglefowl to exhibit age-dependent homophily, where individuals assortatively socialise with those of a similar age (McDonald, Spurgin *et al.* 2019). Indeed, whether differences in temporal trends of aggression between 'young' and 'old' flocks occurred due to the presence of an old individual or simply the presence of a differently aged individual within flocks remains unclear. Future work may test this by conducting social network analyses where hens are added to pre-established flocks containing individuals of an alternative age across multiple flock types (e.g. a young bird added to a group of old birds *vs* an old bird added to a group of young birds). Finally, contrasting temporal trends in aggression between 'old' and 'young' flocks may be explained by varying incentives for competition. For instance, if old females (occupying higher ranks) are more effective at defending food, this could limit access to food for subordinates and prompt increasing aggression over feeding opportunities

across time (MacWhirter 1991). However, the absence of different feeding rates between 'old' and 'young' flocks makes this explanation unlikely.

In flocks supplemented with a male, counts of female-female aggression were initially low and remained stable across the trial period, consistent with previous work in domestic fowl (Lamprecht and Bshary 1994). Though trials took place outside of the breeding season, females in 'male' flocks were occasionally mated and regularly courted. In wild populations, junglefowl breed opportunistically across the dry season, the duration of which may vary across years (Collias and Collias 1967). Combined with captivity, which may relax selective pressures on breeding phenology, this may promote continued, infrequent mating and courtship behaviours outside of periods of reproductive viability (Setchell 1992). Continued sexual harassment may impose costs on females, e.g. by reducing feeding opportunities or risking injury, that are no longer offset by the benefits of reproduction (Leone and Estévez 2008, Carleial, McDonald *et al.* 2019). Increased frequency and duration of perching in 'male' flocks may reflect females' responses to sustained sexual harassment *via* changes to spatial distribution and is consistent with previous work in fowl (McDonald, Spurgin *et al.* 2019). As perching limits agonistic interactions, perpetuated (low) levels of aggression among females may arise until the establishment of dominance hierarchies (dependent on contest outcomes) can occur. If this were the case, declines in female-female aggression would be expected over a longer timescale in mixed-sex flocks; a possibility that should be explored in future studies.

Although feeding activity did not vary across flock types, sexual harassment in 'male' flocks may have increased females' energetic demands and encouraged low levels of aggression to endure. Specifically, increased perching may have constrained females from achieving optimal feeding rates, which might have been higher in these flocks if avoidance of copulation and courtship is

energetically costly. Indeed, the costs of male presence on females' condition has been previously noted in fowl, with higher rates of weight loss found for hens in mixed-sex (*vs* single-sex) flocks (Bhagwat and Craig 1979). Increased energetic requirements may have encouraged sustained (*albeit* low) levels of aggression in 'male' flocks if this led to the perception of food as a limited resource. When access to a resource is limited, dominant individuals should benefit more from monopolising this resource and aggression between hens in 'male' flocks may have reflected competition for improved social rank and food access (Hodge, Thornton *et al.* 2009). Alternatively, low levels of aggression in the presence of a male may alternatively indicate male intervention in female competition as a mediator of sexual conflict (Davies 1986, Ren, Yan *et al.* 1991, Watts 1992, Walter and Trillmich 1994, Schradin and Lamprecht 2000, Kahlenberg, Thompson *et al.* 2008). This has been previously documented for domestic fowl, for example Ylander and Craig (1980) reported a male placing his head and shoulders between two females with his head closer to the more aggressive hen. However, no instances of male intervention into female agonistic interactions were found in our study.

Across flock types, aggression was predicted to decline over successive trial days as initial agonistic interactions lead to the establishment of stable dominance hierarchies (Tibbetts, Pardo-Sanchez *et al.* 2022). Contrary to this prediction, a decline in aggression was only observed for 'young' flocks and not for 'old' or 'male' flocks, which showed stable and increasing instances of aggression over trial days respectively. As flock type did not alter hierarchy stability, it is unlikely that differences in temporal trends of aggression were driven by changes in the time taken for hierarchy establishment. Red junglefowl hierarchies are typically established within three days in small flocks (Carleial, McDonald *et al.* 2019), with occurrences of aggression declining within hours of flock formation (Väisänen and Jensen 2004). In this study, low frequencies of agonistic

avoidances meant social ranks could only be inferred every three days, allowing only one measure of hierarchy stability to be taken across each 6-day trial. Measures of hierarchy stability in this study might therefore have been too coarse to detect initial or subtle differences in stability that might explain varying temporal trends in aggression across flock types. Alternatively, these results may suggest that the social environment can modulate aggression independently of the stability of social hierarchies.

As preening may function as a self-grooming behaviour to relieve stress (Kozak, Rozempolska-Rucińska *et al.* 2019), this behaviour was expected to increase in flocks with higher levels of intrasexual aggression. However, in this study, preening activity was shown to be inversely related to counts of aggression across flock types. One explanation for this is that preening functions as a delayed indicator of stress resulting from aggression in the preceding days. If this were the case though, it is unlikely there would be differences in preening activity between flock types on the initial day of trials. Alternatively, these results may be related to how we defined preening. In this study, the definition of preening included dustbathing, a related grooming behaviour which can involve preening. When dustbathing occurred, it frequently incited agonistic interactions through females evicting each other from bathing sites (H. J. P. O personal observation). As dustbathing can encourage opportunities for agonistic interactions, this behaviour may have been avoided during periods where intrasexual aggression was already high. Further, if aggression was already elevated within a flock, females might avoid preening behaviours if these reduce vigilance of approaching aggressors (Li, Zhou *et al.* 2015). Future studies recording preening and dustbathing separately could disentangle patterns of these behaviours in response to female intrasexual aggression.

4.6 Conclusion

Studies are accumulating that address how the presence of a dominant individual shapes patterns of agonistic interactions within a social environment. However, much of this work considers male intrasexual aggression and may be difficult to generalise when the costs of agonistic interactions differ between the sexes. In this study, we show that the sex- and age-composition of red junglefowl flocks appears to be an important modulator of female intrasexual aggression, resulting in behavioural changes that reflect or encourage different temporal trends of agonistic interactions. Stable, low levels of aggression in flocks containing a male (dominant sex) may have resulted from sexual harassment increasing females' energetic requirements and allowing females to benefit from sustained aggression over time, despite no resulting increase in feeding behaviour. Between 'old' and 'young' flocks there was no difference in the dominance of top-ranked individuals, though contrasting temporal trends of aggression may have come from old hens being less sociable and obtaining higher social ranks than supplemented young hens. Within some flock types, measures of aggression, perching and preening varied over time, highlighting the importance of temporal changes to assess the immediate and longer-term responses by females to their social environment. Altogether, the results of this study suggest females are responsive to their social environment; though not always in accordance with predictions based on male hierarchical organisation. Future studies should therefore take care to further distinguish sex-specific differences in the regulation of agonistic behaviour.

4.7 Appendix C: Supplementary Material for Chapter 4

C.1 Supplementary Methods

CORE GROUP	EXPOSURE 1	EXPOSURE 2	EXPOSURE 3
A	 YOUNG FEMALE (Y)	 OLD FEMALE (O)	 MALE (M)
B	Y	O	M
C	M	O	Y
D	O	Y	M
E	O	*NA*	*NA*
F	M	*NA*	*NA*
G	Y	O	*NA*
H	M	O	M
I	Y	M	O
J	O	Y	M

Figure C.1: The order in which the core groups of 4 young females were exposed to a supplemented individual (a young female, old female or male) to create different flock compositions.

Table C.1: Ethogram of aggressive behaviours and avoidances.

Behaviour	Description
Fight	Two birds peck/lunge or jump and kick with their feet at each other. Between lunges/jumps they may stand facing each other with heads lowered and tails fanned. The first individual to stop and move away by 2 body lengths is the loser.
Display	Two birds stand facing each other with heads lowered and tails fanned. They may additionally puff their chests and sway towards each other without making physical contact (physical contact e.g. pecks/lunge/jump/kick would escalate this behaviour to a fight). The first individual to stop and move away by 2 body lengths is the loser.
Chase	Aggressor runs after target- both moving simultaneously in the same direction- for at least 3 steps. Do not record if target has food in mouth, females often 'parade' food around which invites chasing, but this is not necessarily aggressive.
Lunge	A jabbing movement (including flight towards) of the whole body by aggressor towards target. Physical contact is made between the aggressor and target *or* aggressor may run >3 steps in pursuit of target. If lunge occurs alongside peck, classify as lunge.
Peck	Rapid downward movement of aggressor's beak towards target, often directed at target's head. Do not include exploratory pecks which are gentler. If peck occurs and leads to displacement, classify as peck. If the individual needs to step to reach the target, classify as a lunge.
Displace	Initiator approaches stationary or slowly moving target and reaches a proximity of 1m or closer without no physical contact between the initiator and target. Target moves away by at least 1 body length within 10 seconds and is not followed by the initiator.

C.2 Supplementary Results

Table C.2: Post-hoc comparisons of counts of aggression between flock types on trial days 1 and 6. *t*-ratios, degrees of freedom (df) and post-hoc adjusted *p*-values are shown. Significant results ($p < 0.05$) are indicated in bold.

Trial Day	Flock Type Contrast	*t*-ratio	df	Adjusted *p*
1	Male / Old	0.077	887	0.997
	Male / Young	**-3.400**	**887**	**0.002**
	Old / Young	**-3.745**	**887**	**0.001**
6	Male / Old	-0.912	887	0.633
	Male / Young	**2.905**	**887**	**0.011**
	Old / Young	**4.016**	**887**	**<0.001**

Table C.3: Summarising statistical outputs for GLMMs investigating changes in female intrasexual aggression in (a) response to flock type ('old' *vs* 'young' flocks); and (b) flock types over time. For each GLMM, a summary statistic, degrees of freedom (df) and (adjusted) *p*-values are shown. Significant results ($p < 0.05$) are indicated in bold.

(a)	**Response Variable**	χ^2	**df**	***p***
	Flock Type	**22.632**	**1**	**<0.001**
	Day	**5.104**	**1**	**0.024**
	Familiarity	**4.747**	**1**	**0.029**
	Perching Time	0.027	1	0.869
	Flock Type *Day	**25.125**	**1**	**<0.001**
(b)	**Temporal Trend**	***t*-ratio**	**df**	**Adjusted *p***
	'Old' Flock	**2.259**	**1011**	**0.024**
	'Young' Flock	**-4.728**	**1011**	**<0.001**

Chapter 5: *Social drivers of male coalitions: a theoretical model investigating the role of female quality*

Hannah Ogden, Tommaso Pizzari, Jonathan Green & Eleanor Bath

Author contributions: I conceived of the study and wrote the simulation code and chapter. The chapter was edited to incorporate comments from Tommaso Pizzari, Jonathan Green and Eleanor Bath.

5.1 Abstract

Theoretical modelling of competitive strategies is an important tool for identifying key factors that underlie social behaviours and generating predictions for empirical testing. In many species, males compete for mating opportunities by forming cooperative coalitions that function to exclude rivals. Previous theoretical work has predicted that patterns of coalition emergence should be shaped by social factors, including sex ratios, which alter the intensity of intrasexual competition within a population. Previous work, however, has not considered that reproductive quality can vary substantially among individual females, and that this variation may generate nuance in patterns of coalition formation. Here, we present an individual-based theoretical model where males can join, expand and leave coalitions; and investigate the effects of varying female (reproductive) quality alongside other social factors (variance in male competitive ability, population size, sex ratio and the distribution of rewards within coalitions). Running simulations across a broad parameter space,

we show that introducing variance in female quality promotes on average larger coalitions and more variability in coalition size. Further, we predict that increasing female quality generates greater instability of coalitions, especially under male biased sex ratios and when rewards are distributed more evenly across members of a coalition. Finally, we compare model predictions to reported patterns from previously published data from bottlenose dolphins (*Tursiops aduncus*) and yellow baboons (*Papio cynocephalus*) and discuss the accuracy of our predictions against reported patterns. Altogether, we demonstrate the importance of considering variance in female quality for future theoretical and empirical work investigating male coalitions. Reproductive strategies driven by intrasexual competition should, in part, depend on the interplay between sexes, and incorporating variance in female quality is an important step towards understanding these patterns.

5.2 Introduction

In environments where resources such as food and mates are limited, selection is expected to favour competitive strategies that allow individuals to exclude rivals and monopolise resources (Birch 1957). The occurrence of cooperation, which involves individuals providing help at a cost to themselves, in such environments thus appears paradoxical (Clutton-Brock 2009). Cooperation can evolve when the inclusive fitness benefits of cooperation exceed those obtained through purely selfish strategies, (Hamilton 1964). Under certain conditions, cooperation can also emerge among unrelated individuals, driven solely by direct fitness benefits. For example, when variation in individuals' ability to acquire resources ('resource holding potential') dictates the outcome of contests, cooperation may compensate for these differences, allowing less competitive individuals to access otherwise unobtainable rewards (Harcourt and de Waal 1992). In males, where reproductive success is typically closely tied to mating rate, cooperation for access to mating opportunities can evolve (Clutton-Brock and Parker 1992, Díaz-Muñoz, DuVal *et al.* 2014). Indeed, such displays of male reproductive cooperation – including coordinated displays to attract mates (e.g. Krakauer 2005), cooperative parental care (e.g. Martin and Taborsky 1997) and competitive coalitions where males collectively defend females from rivals (e.g. Connor, Smolker *et al.* 1992) – are observed across a phylogenetically diverse set of clades (Olson and Blumstein 2009, Díaz-Muñoz, DuVal *et al.* 2014).

Among the displays of male reproductive cooperation, competitive coalitions (hereafter 'coalitions') may allow males to improve access to reproductive opportunities by outcompeting rivals (e.g. Colombian white-faced capuchin, *Cebus capucinus*, Perry 2012) or indirectly by attaining higher social ranks that may increase both access and propensity to attract mates (e.g.

spotted hyenas, *Crocuta crocuta*, Engh, Siebert *et al.* 2005; and rhesus macaques, *Macaca mulatta*, Altmann 1962). Male coalitions are particularly diverse (Díaz-Muñoz, DuVal *et al.* 2014). For example, males can form coalitions ranging in size from two (e.g. tessellated darters, *Etheostoma olmstedi*, Stiver, Wolff *et al.* 2013; yellow baboons, *Papio cynocephalus*, Noë 1990) to fourteen individuals ('superalliances' of bottlenose dolphins, *Tursiops aduncus*, comprised of multiple coalitions, Connor, Heithaus *et al.* 2001). Further, coalitions may be short-lived, for example where males cooperate against a rival in a single contest (e.g. Barbary macaques, *Macaca sylvanus*, Bissonnette, de Vries *et al.* 2009), or long-lived, with associations among males (often termed 'alliances') persisting outside of competitive contexts, in some cases for multiple years (e.g. Camargue horses, *Equus caballus*, Feh 1999). Even within species, the size and stability of coalitions may vary, depending in part on the availability and competitiveness of cooperative partners (Whitehead and Connor 2005, Olson and Blumstein 2009). Based on these and other empirical studies, we have a good understanding of the diversity of coalitions within and across populations and species, but as of yet our ability to explain this diversity is more limited.

To address this, a number of theoretical models have been developed, which seek to understand coalition formation in males (reviewed in Bissonnette, Perry *et al.* 2015). In the majority of these models, individuals pursue optimal strategies based on the assumption that coalition formation is associated with certain benefits and costs. Such models have been useful in understanding which individuals should form coalitions (Pandit and van Schaik 2003) and when (van Schaik, Pandit *et al.* 2004), and how the outcome of previous interactions should influence the probability of coalition formation between partners (Gavrilets, Duenez-Guzman *et al.* 2008). Other models have considered how population size and structure may predict the emergence of coalitions (Whitehead and Connor 2005, Gavrilets, Duenez-Guzman *et al.* 2008). For example, Whitehead and Connor

(2005) showed that the optimal size of coalitions depended upon the number of males competing for a female (denoted by *m*), but not variation in resource holding potential, population size or the distribution of reproductive success within the coalition. Absent, however, from theoretical treatments of coalition formation to date is a consideration of how the reproductive value of the females over which males compete influences coalition dynamics and contributes to explaining variation in coalition patterns.

Variation in resource value has long been recognised as an important modulator of competition, including competition between males for mates (Arnott and Elwood 2009). By showing preference for females associated with higher reproductive returns, males can offset costs associated with reproduction (e.g. investment into ejaculate production, Wedell, Gage *et al.* 2002; or mate guarding, Sparkes, Keogh *et al.* 1996) (Kraak and Bakker 1998). For example, males may prefer females with traits signalling higher fecundity (e.g. large size, Byrne and Rice 2006; sexual receptivity, Domb and Pagel 2001; or virginity (associated with a lower risk of sperm competition in species with first-male sperm precedence, Simmons, Llorens *et al.* 1994). Increased competition for higher quality females by males is thus expected, with competitive strategies, such as the formation of large coalitions, emerging to exclude rivals from this resource. However, when competition for preferred females is intense, the likelihood of achieving reproductive success may be reduced if the rewards of coalition formation are shared across multiple partners. As such, males should distribute themselves across females of different quality (and in coalitions of different size) according to an ideal free distribution such that the reproductive return of individual males becomes approximately similar across the population (Jordan, Kokko *et al.* 2014). Increased variation in female quality is thus expected to generate a broader distribution of coalition sizes, with the size of coalitions reflecting the quality of the contested female. This may additionally

result in a greater instability of coalitions if there are multiple strategies by which males can improve their reproductive returns and the most beneficial strategy depends on the composition of coalitions within the social environment.

The strategy a male pursues may depend on his relative competitive ability (rank) within a population. For example, in yellow baboons, low-ranking males are often unsuccessful in finding coalition partners whereas high-ranking males often do not require coalitions to successfully reproduce (Noë and Sluijter 1995). Whether these patterns depend on the variance in female quality of a population is not yet known, though we may expect high variance in female quality to exaggerate this trend if mid-ranking males more consistently benefit from forming large coalitions to access high quality partners. Conversely, high-ranking males may benefit from forming coalitions when populations contain few high-quality females that are heavily contested and impossible for males to obtain alone. Altogether, a male's decision to cooperate with other males is expected to depend on his own competitive ability while being sensitive to information on female quality. As such, incorporating the effect of variation in female quality in theoretical models should allow for a better understanding of the conditions necessary for the emergence and composition of coalitions.

In this study, we develop an individual-based model to determine the influence of varying female quality on coalition formation. To do this, we simulated closed populations in which males are repeatedly given the opportunity to enter and leave coalitions to access mating opportunities with females of varying quality. Using this model, we first investigated the role of varying female quality in modulating the size and stability of male coalitions. We describe the influence of varying female quality across a range of social environments where male competitive ability, population size, sex ratio and the distribution of reproductive gains away from subordinate males within a

coalition (i.e. reproductive skew) were varied. We predicted high variance in female quality would lead to larger, more unstable coalitions when variance in male competitive ability was also high (males should form larger coalitions to overcome stronger opponents for access to high quality females) or when populations were large (more available partners may increase coalition instability). Alternatively, we predicted the effects of high variance in female quality would be limited under a female biased sex ratio, if access to reproductive opportunities does not require coalition formation, or when high reproductive skew reduces the benefits of coalition formation for subordinate members. Next, we investigated how variation in female quality influenced the relationship between male rank and coalition size and describe these patterns across social environments. Finally, we explored the validity of our model by reviewing the characteristics of coalitions formed in mammalian species and parameterising our model based on bottlenose dolphins and baboons, for which information on variance in female quality is available and coalition dynamics are particularly well described.

5.3 Methods

5.3.1 Model Overview

An individual-based model was produced to understand how variation in female quality interacts with population size, sex ratio, and variance in male competitive ability to modulate patterns of male coalitions. Here, we assumed males exclusively formed coalitions using an 'all-up' tactic, whereby two or more males formed coalitions against a more powerful opponent or coalition (van Schaik, Pandit *et al.* 2004).

At the beginning of a simulation, each male was assigned a value of competitive ability, $c(j)$, selected from a truncated normal distribution (see Model Parameters). In addition, each female was assigned a value of reproductive quality (f) from a separate truncated normal distribution, where higher values indicate a greater likelihood of conception. Males, whether alone or in coalitions, were assumed to consort – that is, have access to mating opportunities - with one female at a time (as seen in e.g. bottlenose dolphins, Connor, Richards *et al.* 1996 and yellow baboons, Bercovitch 1988, though not Carmague horses ,Feh 1999). Consortships were assigned assortatively, such that the male with the highest value of $c(j)$ preferentially consorted with the female with the highest value of f, the male with the second highest value of $c(j)$ preferentially consorted with the female with the second highest value of f, and so on. When there were more males than females in the population, the least competitive males were not assigned a consortship at the beginning of the simulation. Similarly, when there were more females than males in the population, females of the lowest quality were not assigned a consortship at the beginning of the simulation.

Each simulation consisted of 100 time-steps. Within each time step, all males within a population were considered a focal male in turn, and the order of turns was randomised. If the focal male was alone, he could either remain alone or join another male or coalition. If the focal male was already a member of a coalition, he could remain in that coalition, combine his coalition with another male/coalition, or leave the coalition (alone) to either be alone or merge with another male/coalition (see **Figure 5.1**). The collective competitive ability of a coalition was determined by the sum of competitive abilities of all its members ($c(i) = \sum c(j: j \in i)$) (Noë 1992, Whitehead and Connor 2005, Stamatopoulos, Sengupta *et al.* 2009). A coalition would automatically take over a consort with the highest quality female where $c(i)$ exceeded the competitive ability of the

male or coalition already in consort with that female. If there were multiple consorts of this description available, the coalition would take over one of these consorts at random.

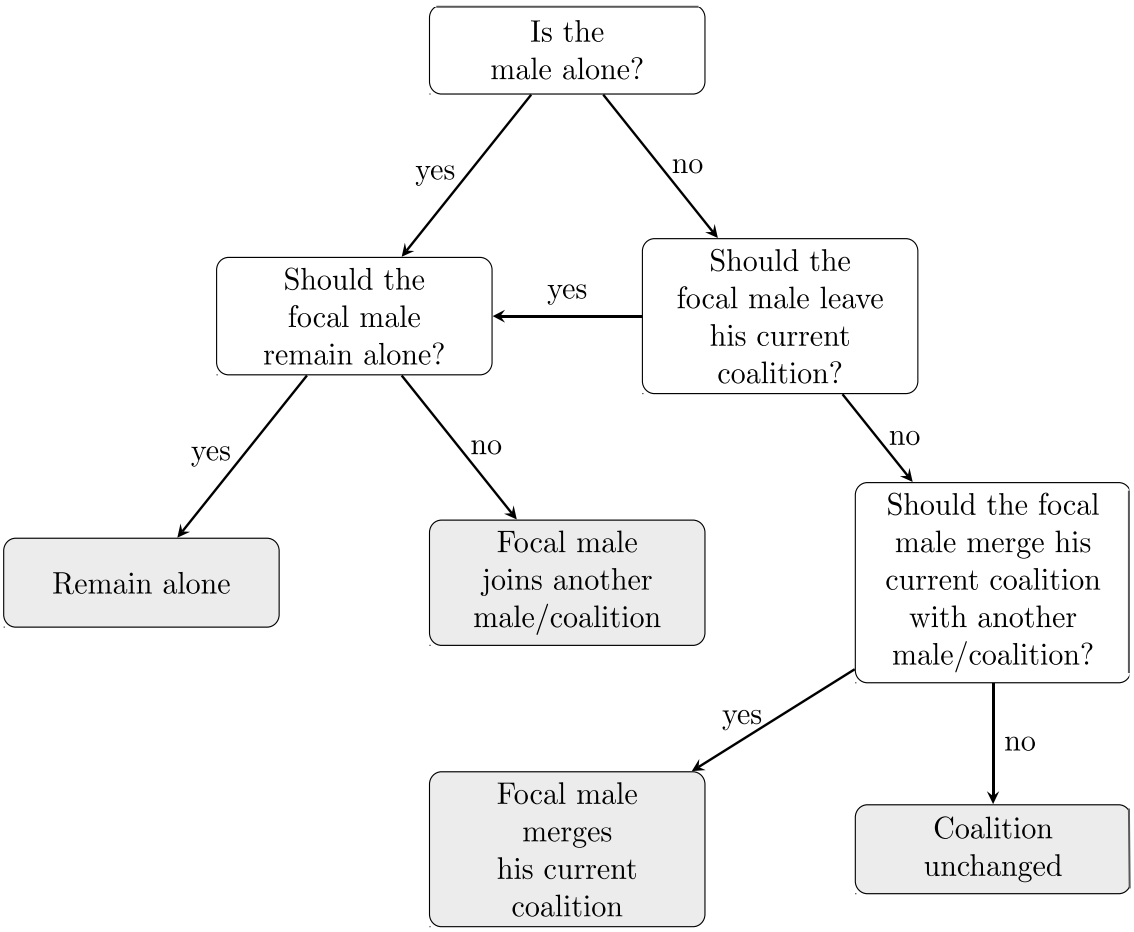


Figure 5.1: The decision tree followed by each male within a time-step. Individuals make decisions to maximise their payoffs (p). White boxes denote decision nodes and grey boxes denote outcomes.

The decision a male made to join, leave or merge coalitions depended on which option (strategy) yielded them the highest payoff and whether this payoff was greater than that which they currently received. The payoffs (p) a male received were calculated according to the following rules:

- Males in the population were assumed to have perfect knowledge of their own $c(j)$ and that of others. This knowledge allowed a male to understand the ranked value of $c(j)$ he would have upon joining any coalition.
- Within coalitions, male reproductive payoffs were skewed towards the most dominant (i.e. top-ranked) male. For dominant males (whose rank (r) within a coalition is 1), payoffs were calculated as: $p_{r=1} = s \cdot f$, where s denotes a value of reproductive skew between 0 (dominant males receive no reproductive opportunities) and 1 (dominant males monopolise reproductive opportunities). Remaining reproductive opportunities were then shared equally between remaining males ($r > 1$), such that: $p_{r>1} = \frac{(1-s)\cdot f}{n_i - 1}$, where n_i is the size of the coalition.
- When reproductive skew was equal, reproductive payoffs were equally shared between coalition members, $s = \frac{1}{n_i}$.
- When a male consorted a female alone (i.e. not in a coalition), $p = f$.

When a male's best strategy involved joining or merging a coalition, this was only possible if the partner male or at least half the members within a partner coalition received a higher payoff as a consequence of this action. Thus, a solitary male 'agreed' to enter into a coalition only if his payoff increased as a result of allowing the focal male to join him (i.e. both partners benefit), while an existing coalition 'agreed' to expand to include the focal male only if the majority of individuals within the existing coalition gained a greater payoff as a consequence (van Schaik, Pandit *et al.*

2006). To ensure males did not become 'stuck' attempting to pursue strategies that were continuously rejected by prospective partners, males were occasionally required to choose suboptimal strategies. Specifically, if the composition of males within a population did not change from one time-step to the next, males were not allowed to pursue a partner that had rejected them in the previous time-step. Instead, males pursued the strategy with the second most profitable payoff.

When takeovers successfully occurred, consortships were redistributed to reflect changes in $c(i)$. Specifically, when a male or coalition took over a consort, the displaced male or coalition would enter a consort with the next highest quality female, displacing any male or coalition with lower $c(i)$ associated with this female, and so on.

5.3.2 General Model Parameters

We ran a number of simulations varying the following social parameters:

- **Variance in female quality**: the standard deviation of the normal distribution from which values of f were selected was varied. Values of f were selected from a truncated normal distribution, bound between 0.01 and 0.99 with a mean of 0.5, and the standard deviation of this distribution was set at 0, 0.1 or 0.5. Standard deviations of 0.1 and 0.5 were selected based on empirical studies suggesting that these are moderate and extreme variations of female quality (see Case Studies).
- **Variance in male competitive ability**: values of $c(j)$ were selected from an identical truncated normal distribution, again with a standard deviation of 0, 0.1 or 0.5.

- **Population size**: populations contained 6 (hereafter 'small'), 12 (hereafter 'medium') or 24 (hereafter 'large') males. For simplicity, we assumed that populations were outbred, and males were unrelated to each other. Values of population size (as well as values of sex ratio and reproductive skew below) were selected to fall within the range reported for mammalian species (see **Table 5.1**).
- **Sex ratio**: the number of females was varied to produce sex ratios of 5:1, 3:1, 1:1 and 1:2 males *per* female.
- **Reproductive skew**: reproductive rewards were shared within coalitions equally or by varying s (i.e. the proportion of matings skewed towards the top-ranked male) between 0.5, 0.75 and 0.99.

This produced 432 combinations of social parameters across which we assessed how variation in female quality influenced coalition size, stability and the relationship between male rank and coalition size. As the outcome of simulations depended on the selected values of $c(j)$ and f, as well as the order in which individual males were chosen, each combination of simulations was run 20 times. This allowed us to quantify the variation around estimates of coalition size, stability and the size of coalitions associated with each male rank. Overall, 8,640 simulations were run.

5.3.3 General Model Outputs

Between each successive time-step, a binary measure of coalition stability was recorded. A stability value of 0 denoted that the composition of males within and across coalitions changed between adjacent time-steps due to a male leaving, joining or merging coalitions. A stability value of 1 denoted that the composition of males within and across coalitions did not change between consecutive time-steps. To compare coalition stability across social parameters, stability measures

were averaged within and then across simulations for each combination of social parameters. For each combination of social parameters, the mean and standard error of the average coalition stability was recorded.

At the end of each time-step, information on the size of the coalition each male was associated with was recorded (a coalition size of 1 denotes males that are alone). To compare differences in coalition sizes across social parameters, the median coalition size within each time-step was recorded for each simulation. Median coalition sizes were then averaged across time-steps and across simulations for each combination of social parameters. For each combination of social parameters, the mean and standard error of the average coalition size was recorded.

To compare the relationship between male rank and the size of the coalitions they most often entered, males within each simulation were ranked by their competitive ability (with rank 1 being the male with the highest competitive ability). When two or more males shared equal values for competitive ability, rank was randomly assigned within these males. For individual males, the size of the coalition they were in at each time-step within a simulation was averaged. Across simulations, for each combination of social parameters, mean coalition size was averaged within each male rank. To allow comparisons across populations of varying size, males were placed into 3 ‘grouped ranks’ of ‘low’, ‘mid’ and ‘high’, indicating whether males were in the bottom, middle or highest third of ranks within the population respectively. For each combination of social parameters, the mean and standard error of the averaged median coalition size for each grouped rank was recorded.

5.3.4 Case Studies

We collated empirical data on species with male coalitions to identify a suitable set of species to parameterise our model and test its validity. While coalitions occur over a diverse array of taxa (including fish, Stiver, Wolff *et al.* 2013; and birds, Krakauer 2005), we focused on reviewing coalitions within mammalian species as these are particularly well described (e.g. Olson and Blumstein 2009, Díaz-Muñoz, DuVal *et al.* 2014, Smith, Jaeggi *et al.* 2023). Collating this information additionally informed levels within some general parameters of the model (population size, sex ratio and reproductive skew) listed above.

A list of mammalian species where males form coalitions was identified from a recent review (Smith, Jaeggi *et al.* 2023). Below, we review details (purpose and size) of these species' coalitions. For each species, we used the term "(alliance OR coalition) AND male AND (*species name*)" to search within the title, abstract or keyword of articles (summarised in **Table 5.1**). While coalitions forming principally to challenge or maintain dominance hierarchies may secondarily improve access to females, following Díaz-Muñoz *et al.* (2014) we considered these to be functionally distinct from coalitions primarily involved in female access or defence. Species that formed coalitions for the primary purpose of female access and defence were identified as candidate case studies for our model. We excluded two species (*Saimiri boliviensis* and *S. oerstedii*), in which coalitions aid in access to females, but also confer other benefits including protection from predation and access to food (Boinski, Kauffman *et al.* 2005), as it was not clear that reproductive benefits are the primary driver of coalition formation in these species. We also limited our set of candidate species to those where reproductive benefits are shared solely among members of the coalition, allowing a within-coalition measure of reproductive skew to be

calculated. Finally, because our model assumes that males (or coalitions) are unable to consort with more than one female simultaneously, species in which males are able to monopolise multiple females simultaneously were excluded from our set of candidate species.

Four candidate species were identified: Indo-Pacific bottlenose dolphins, yellow baboons, olive baboons (*Papio anubis*) and barbary macaques. Barbary macaques were subsequently excluded as very few coalitions in this species are defined as using an 'all-up' tactic (9.8% of coalitions were all-up in one reported population, (Young, Majolo *et al.* 2014)). In our model, less competitive males form coalitions to outcompete more competitive males or coalitions in an 'all-up' configuration. Thus, our model is not well positioned to explore drivers of coalition formation in this species.

Table 5.1: Summary information on population and coalition structure for species forming male intragroup coalitions. This is not intended to be an exhaustive summary but is instead intended to illustrate some general characteristics of coalitions across species. Species where the selective advantage of coalition formation is unknown (or else not stated) are omitted. Where available, values of reproductive skew are calculated from paternity data (underlined). Otherwise, reproductive skew estimates are based on observed matings. When the primary purpose of a coalition was not related to female access or defence, information on whether coalitions consorted single females and how reproduction was skewed within coalitions was considered non-applicable (shown by 'NA').

Species	Study population			Coalition description			References
	***n* mature males**	***n* mature females**	**Size range**	**Primary purpose**	**Single consort?**	**Reproductive skew**	
Alouatta palliata	3-4 (mean 3.5)	4 (mean 4)	2	Female access/defence	N	Unreported	Dias, Rangel-Negrin *et al.* 2010
Alouatta seniculus	Unreported	Unreported	2-4	Female access/defence	N	100% to alpha	Pope 1990
Cebus capucinus	1-13	2-11	2+[1]	Female access/defence	N	74%[2] to alpha	Perry 2012
Chlorocebus pygerythrus	Unreported	Unreported	2-3	Unclear[3]	NA	NA	Freeman, Young *et al.* 2016
Colobus vellerosus	Unreported	Unreported	2-3	Female access/defence	N	87.5%[2] to alpha	Teichroeb, Wikberg *et al.* 2014
Crocuta crocuta	7-17	13-26	2	Challenge/maintain social hierarchy	NA	NA	Engh, Siebert *et al.* 2005
Equus caballus	Unreported	Unreported	2-5	Female access/defence	N	75% to alpha	Feh 1999

Equus ferus	6-10	0	2	Challenge/maintain social hierarchy	NA	NA	Krueger, Schneider *et al.* 2015
Eulemur fulvus	2-4 (mean 2.8)	2-7 (mean 3.8)	2-3	Female access/defence	N	66%[2] to alpha	Ostner and Kappeler 2004
Lycaon pictus	10	9	2	Challenge/maintain social hierarchy	NA	NA	de Villiers, Richardson *et al.* 2003
Macaca arctoides	Mean 19.4	Mean 24.8	2	Female access/defence	N	Equal[5]	Toyoda, Maruhashi *et al.* 2022
Macaca assamensis	12	12	2+[1]	Challenge/maintain social hierarchy	NA	NA	Schülke, Bhagavatula *et al.* 2010
Macaca fascicularis	Unreported	Unreported	2	Female access/defence	N	Unreported	Engelhardt, Heistermann *et al.* 2006, Gerber, Krützen *et al.* 2016
Macaca fuscata	3	6	2+[1]	Challenge/maintain social hierarchy	NA	NA	Kawazoe 2021
Macaca mulatta	38-41	Unreported	2-7	Challenge/maintain social hierarchy	NA	NA	Higham and Maestripieri 2010
Macaca nigra	7-18	Unreported	2-6	Challenge/maintain social hierarchy	NA	NA	Neumann, Kulik *et al.* 2022
Macaca sylvanus	24	27	2-3	Female access/defence	Y	66% to alpha	Bissonnette, Bischofberger *et al.* 2011
Macaca thibetana	9	13	2	Challenge/maintain social hierarchy	NA	NA	Berman, Ionica *et al.* 2007

Pan paniscus	5	11	2-3	Female access/defence	N	62%[2] to most successful sire	Surbeck, Boesch *et al.* 2017
Pan troglodytes	9-11	Unreported	2-3	Challenge/maintain social hierarchy	NA	NA	Gilby, Brent *et al.* 2013
Papio anubis	4-8	18-20	2-3	Female access/defence	Y	Equal	Bercovitch 1988
Papio cynocephalus (HOOK, Amboseli)	6-9	18-19	2-3	Female access/defence	Y	86% to alpha	Noë 1990
Saimiri boliviensis	Unreported	Unreported	Unspecified	Group takeover/defence	NA	NA	Boinski, Kauffman *et al.* 2005
Saimiri oerstedii	Unreported	Unreported	Unspecified	Group takeover/defence	NA	NA	Boinski, Kauffman *et al.* 2005
Tursiops aduncus (Shark Bay)	16	13	2-3	Female access/defence	Y[4]	80% to alpha[6]	Smolker, Richards *et al.* 1992, Krützen, Barré *et al.* 2004
Tursiops truncatus	Unreported	Unreported	2-3	Female access/defence	Y	Unreported	Parsons, Durban *et al.* 2003

[1] Some larger coalitions of unspecified size. [2] Estimates of reproductive skew may include males that remained in residence in groups following a coalition takeover. [3] Despite males within coalitions maintaining close proximity to females, implying reproductive benefits of coalition formation, no mating was observed with the female. [4] One recorded instance of males consorting 2 females simultaneously (Connor, Richards *et al.* 1996). [5] Rewards equally shared among all coalition members. [6] 2/15 coalitions achieved 75% of matings (mean paternity per male = 0.53, variance = 1.27).

Social parameters (group size, variance in male competitive ability and variance in female quality) were gathered for populations of Indo-Pacific bottlenose dolphins (hereafter 'dolphins') and yellow and olive baboons (see **Tables C.1** and **C.2**). For dolphins (Case Study 1), it was possible to parameterise our model using information from one population. Yellow and olive baboons show similar patterns of coalition formation and show some overlap in geographical distribution (Noë and Sluijter 1995, Fuchs, Gilbert *et al.* 2018)). Because more complete information on social parameters was available for yellow baboons (hereafter 'baboons'), this species was chosen for Case Study 2.

For dolphins and baboons, populations that provided information across the most social parameters were used for case studies (described below). For either species, no single publication provided information on all social parameters of interest. Social parameters were therefore gathered by collating datasets from publications across multiple years, where populations were likely comprised of different (or differently aged) individuals.

Reproductive skew for both species was calculated using the B index, which takes into account group size and productivity (here, the number of matings) (Nonacs 2000). For both dolphins and baboons, reproductive skew for multiple coalitions were reported (Noë 1990, Krützen, Barré *et al.* 2004). For each coalition, B was calculated as: $\sum_{i=1}^{n}(p_i - \frac{1}{N})^2 - (1 - \frac{1}{N})/K$, where: p_i is the proportion of the total number of K mating opportunities received by the *i*th member of a group of size N (see Nonacs 2000). Values of B were then standardised by dividing them by B_{max} ($(1 - \frac{1}{N} + (\frac{1}{N} - 1))/K$), that is the value of B expected for that coalition when one individual completely monopolises reproductive opportunities. Standardised values of B were then averaged across coalitions to give a mean value of reproductive skew.

Case Study 1: Dolphins

Information published between 1992 and 2021 on dolphins in Shark Bay, Western Australia was used to parameterise a series of simulations (summarised in **Table 5.2**). In this population, coalitions of 2-3 males are observed herding potentially oestrus females away from rival males or coalitions (Connor, Smolker *et al.* 1992). The population of Shark Bay comprises many hundreds of individuals (Randić, Connor *et al.* 2012), with an adult sex ratio of approximately 1:1 (unpublished data, M. Krutzen). The Shark Bay population consists of multiple parties (spatially cohesive groups where each member is within 10m of any other party member) within which males can select other males as coalition partners (Smolker, Richards *et al.* 1992). On average, parties consist of 16 males and 13 females (Smolker, Richards *et al.* 1992).

Little information exists on variance in male competitive ability, though there is some evidence in juveniles that competitive ability is correlated with body length (Samuels and Gifford 1997). As such, reported values for the mean (202.9cm) and variance (SD = ± 4.16cm) in male body length were used to generate a distribution of competitive ability for males (van Aswegen, Christiansen *et al.* 2019). Distributions of female quality were based on the mean (0.13) and variance (SD = ± 0.07) in the number of calves females produced *per* year (pedigree data obtained from: https://www.monkeymiadolphins.org/family-trees-2/). Paternity data were available from 3 coalitions and were used to calculate an average measure for reproductive skew of 0.8 (Krützen, Barré *et al.* 2004). Within simulated coalitions, this meant dominant males achieved 80% of matings, with the remaining 20% of matings shared equally among remaining coalition members.

Case Study 2: Baboons

Information published between 1975 and 1995 on baboons from the HOOK population in Amboseli Nature Reserve, Kenya was used to parameterise a series of simulations (summarised in **Table 5.2**). In this population, coalitions form among 2-3 males, for the purpose of accessing oestrus females (Noë and Sluijter 1995). In 1990, the population comprised 6-7 adult males and 14-16 adult females (mean values not reported), resulting in a female biased adult sex ratio (Noë and Sluijter 1990). However, in baboon populations, few females undergo oestrus synchronously (2-7 females in the HOOK population; Noë and Sluijter 1990). Thus, the operational sex ratio likely tends to be male biased (Bercovitch 1988). Simulations were repeated for all combinations of sex-ratios with 6-7 males and 2-7 ('receptive') females. Distributions of male competitive ability were based on the mean (10) and variance (SD = ± 3.9) of David's (dominance) scores, calculated from contest outcomes (Hausfater 1975). Distributions of female quality were based on the mean (3.81) and variance (SD = ± 1.56) of the number of times females had cycled (ovulated) since their most recent pregnancy (Fitzpatrick, Altmann *et al.* 2015). Females who have undergone more cycles since their most recent pregnancy are relatively more likely to conceive and are preferentially consorted by males (Fitzpatrick, Altmann *et al.* 2015). Measures of female quality were taken from the general Amboseli population which contains five populations, including two descended from the HOOK population (Alberts, Watts *et al.* 2003). Mating data were available from 4 alliances (Noë 1990) and was used to calculate an average measure for reproductive skew of 0.85. Within simulated coalitions, this meant dominant males achieved 85% of matings, with the remaining 15% shared equally among remaining coalition members.

Table 5.2: Summarising model parameters for sets of simulations investigating coalition formation in dolphins and baboons.

Species	Model Parameters				
	***n* adult males**	**Variance in male competitive ability**	***n* adult females**	**Variance in female fecundity**	**Reproductive skew within coalition**
Dolphins *Tursiops aduncus*	Mean = 16 Smolker, Richards *et al.* 1992	Mean = 202.9 ± 4.16cm (SD) body length van Aswegen, Christiansen *et al.* 2019	Mean = 13 Smolker, Richards *et al.* 1992	Mean = 0.13 ± 0.07 (SD) calves *per* year [1]	80% Krützen, Barré *et al.* 2004
Baboons *Papio cynocephalus*	Range = 6-9 Noë and Sluijter 1990	Mean = 10 ± 3.9 (SD) David's Score Hausfater 1975	Range = 2-7 receptive Noë and Sluijter 1990	Mean = 6.43 ± 0.95 (SD) cycles since last pregnancy Fitzpatrick, Altmann *et al.* 2015[2]	85% to alpha Noë 1990

[1] Information on female fecundity taken from: https://www.monkeymiadolphins.org/family-trees-2/. [2] Data from 'Amboseli population'.

5.4 Results

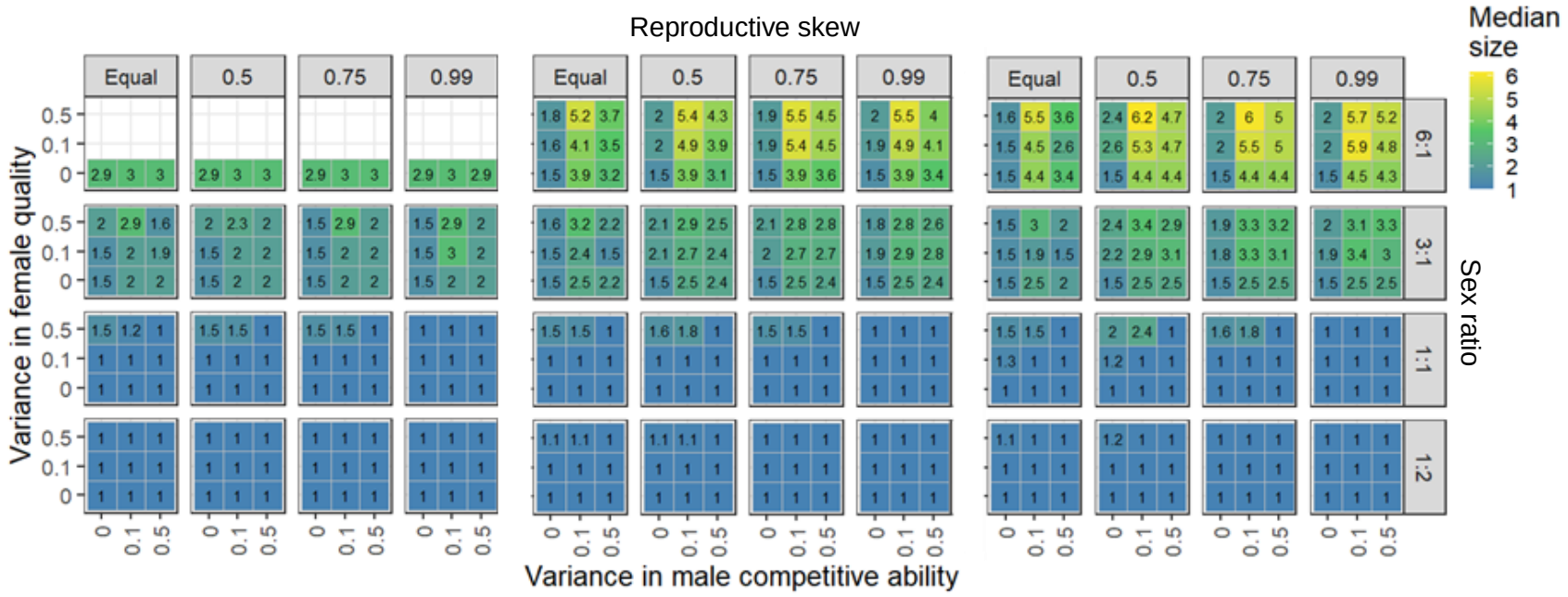
5.4.1 General Findings

A summary for average values of coalition size and stability across parameter combinations is provided in **Table C.3**. Average coalition sizes for each male rank across parameter combinations is provided in **Table C.4**.

Coalition size

Under even and female biased sex ratios, males remained alone (median coalition size of 1), with some exceptions when female variance was high and reproductive payoffs were not highly skewed (i.e. dominant males did not receive a high proportion of reproductive payoffs within a coalition) (bottom two rows of panels in **Figure 5.2**). A further exception occurred in large (24 males) populations with low reproductive skew, where low variance in female quality was also associated with some males forming coalitions (median coalition size >1) (**Figure 5.2c**).

In male biased sex ratios, median coalition size generally increased with increasing variance in female quality. An exception to this trend was seen in medium (12 males) and large populations where the sex ratio was 3:1, there was variance in male competitive ability and rewards were equally shared within coalitions (grids in the first column, second row of **Figure 5.2b** and **5.2c**). In these cases, median coalition sizes were lowest when variance in female quality was low, compared to when variance was high or absent. In addition, as population size increased, the size of coalitions generally increased. Further, under male biased sex ratios, coalitions were largest when variance in male competitive ability was low.



(a) Small (6 males) (b) Medium (12 males) (c) Large (24 males)

Figure 5.2: Median coalition size across populations of different sizes (a: small, 6 males; b: medium, 12 males; c: large, 24 males). Each plot consists of 16 grids containing 9 tiles with the exception of the top row in (a) where simulated populations contained only 1 female and thus female quality could not vary. Each tile provides an averaged value of median coalition size across 100 time-steps from 20 simulations. Across grids, columns specify the reproductive skew (equally shared among coalition members or skewed towards the dominant male, with the remaining share distributed equally among the remaining coalition members) and rows specify the sex ratio (males:females). Within grids, columns denote the standard deviance in male competitive ability around a constant mean ('absent' = 0; 'low' = 0.1; 'high' = 0.5) and rows denote the standard deviance in female quality around a constant mean ('absent' = 0; 'low' = 0.1; 'high' = 0).

Coalition Stability

Generally, coalitions became less stable across a broader range of parameter combinations as populations increased from small to large (**Figure 5.3a-c**). Further, variance in female quality interacted with other social parameters to influence the stability of male coalitions. Under an even sex ratio (1:1), stability depended on an interaction between variance in female quality, reproductive skew and population size (**Figure 5.3a-c**). Coalitions were less stable when variance in female quality was high, but as population size increased, this effect was increasingly limited to cases where reproductive skew was low ('Equal' and '0.5' grid columns in **Figure 5.3b-c**). When the sex ratio was moderately male biased (3:1 sex ratio), coalitions became less stable as variance in female quality increased (**Figure 5.3a-c**). This trend was more apparent when reproductive skew was low, as coalitions forming under these conditions were generally less stable. When the sex ratio was heavily male biased (6:1 sex ratio), variance in female quality had little discernible effect on the stability of coalitions across levels of reproductive skew in small and medium-sized populations (**Figure 5.3a-c**). In contrast, for large populations, the influence of varying female quality depended on the level of reproductive skew. These patterns were similar to those observed in the 3:1 sex ratio, with the exception that variance in female quality had little effect on stability when reproductive payoffs were equally shared among all members of a coalition.

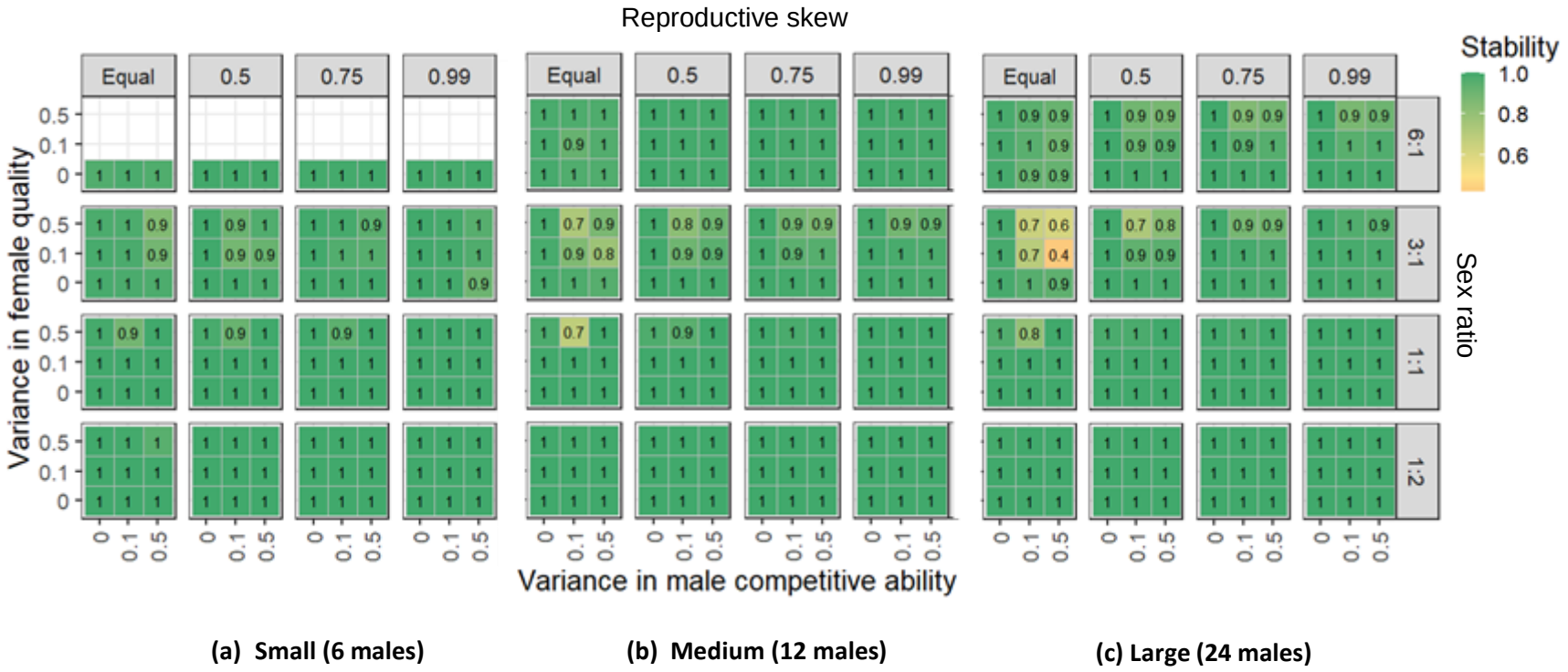


Figure 5.3: Stability of coalitions across populations of different sizes (a: small, 6 males; b: medium, 12 males; c: large, 24 males). Each plot consists of 16 grids containing 9 tiles with the exception of the top row in (a) where simulated populations contained only 1 female and thus female quality could not vary. Each tile provides an averaged value of coalition stability from 20 simulations. Coalition stability describes the proportion of adjacent time steps where the composition of coalitions changed. Across grids, columns denote the reproductive skew (equally shared among coalition members or skewed towards the dominant male, with the remaining share distributed equally among the remaining coalition members) and rows specify the sex ratio (males:females). Within grids, columns denote the standard deviance in male competitive ability around a constant mean ('absent' = 0; 'low' = 0.1; 'high' = 0.5) and rows denote the standard deviance in female quality around a constant mean ('absent' = 0; 'low' = 0.1; 'high' = 0).

Male rank and coalition size

Across combinations of social parameters, there was no strong indication that male rank was associated with coalition size (see **Table C.4**). In other words, a male's rank (dictated by his relative competitive ability) did not appear to influence the decision a male made on whether to remain alone or be part of a coalition of any particular size.

5.4.2 Case Studies

Simulated populations were parameterised using species data including information variance in female quality. Below we outline predictions on coalition size, stability and the relationship between male rank and coalition size generated from these data and later evaluate their applicability (see Discussion).

Case Study 1: Dolphins

Observational data indicates that dolphins frequently form coalitions of 2-3 males. In our simulated populations, coalition size ranged from 2-4 individuals, though many males remained alone, resulting in an average median size of 1.74 (± 0.06 SE) members. Across time-steps, these populations remained largely stable (mean stability = 0.98 ± 0.01), consistent with observations that coalitions in natural populations can remain stable for years (Connor 2007). In **Figure 5.4**, an example of the distribution of coalition sizes across time-steps within one simulated dolphin population is shown. In addition, low-ranking males were predicted to form coalitions less frequently (leading to a smaller coalition size of 1.81 ± 0.09 members) than males of 'mid' and 'high' ranks (1.61 ± 0.08 and 1.49 ± 0.07 members respectively).

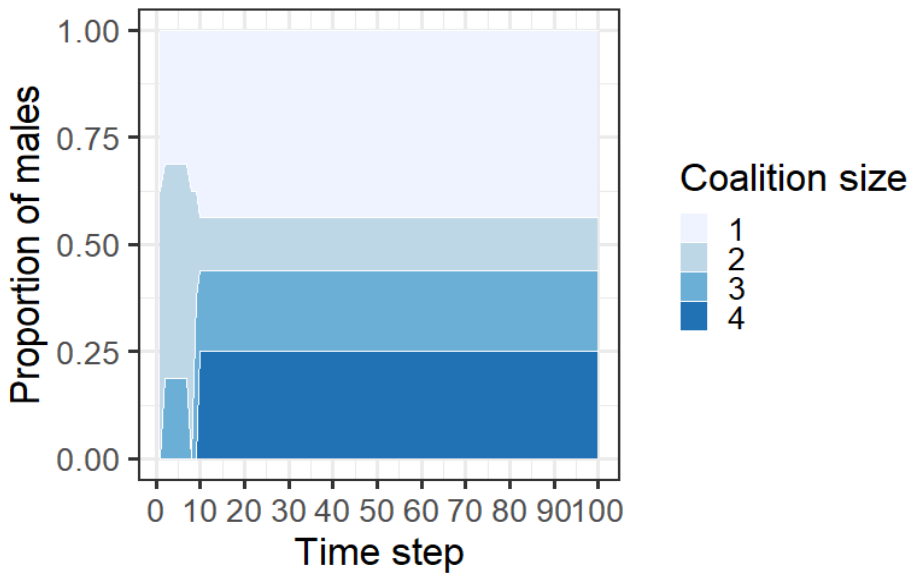


Figure 5.4: The distribution of coalition sizes across time-steps for one simulated dolphin population.

Case Study 2: Baboons

Observational data indicate coalitions form fairly frequently within baboon populations and contain up to 3 individuals (Noë and Sluijter 1990). Coalition sizes predicted from our simulations are mostly consistent with this range, with the exception of even and heavily male biased sex ratios where males are invariably alone or the median coalition size exceeds 3 members (see **Table C.5** and **Figure 5.5**). Similar to predictions for dolphin populations, simulated coalitions in baboons were highly stable (mean stability = 0.96 ± 0.02). Finally, 'high' ranked males were generally members of smaller coalitions than 'low' and 'mid' ranked males, though the strength of this relationship depended upon the population size and sex ratio (see **Table C.6**).

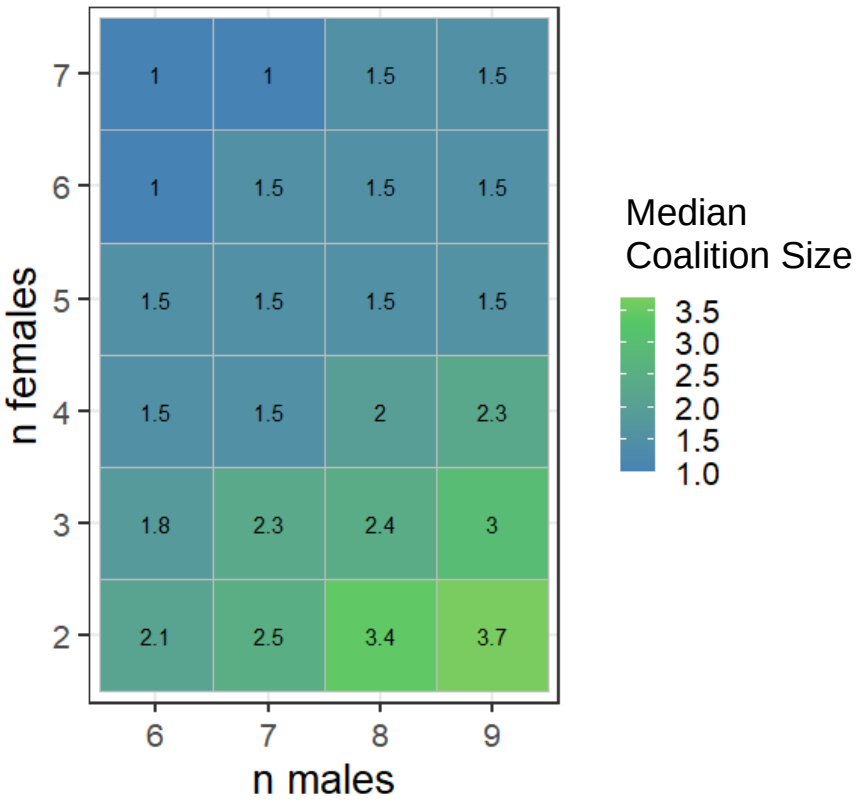


Figure 5.5: Summarising the median size of coalitions across simulated baboon populations containing 6-9 males and 2-7 females. Each tile provides an averaged value of median coalition size across 100 time-steps from 20 simulations.

5.5 Discussion

Variation in female quality is an important predictor of patterns in male mating behaviour. However, little is understood about how variance in female quality modulates a male's decision to cooperatively compete for reproductive opportunities through coalition formation. In this study, we used individual-based simulations to understand whether variance in female quality – in combination with other social drivers – alters the size and stability of male coalition formation and the relationship between male rank and coalition size. Our results predict larger coalitions should emerge where there is greater variance in female quality. In addition, we show the extent to which coalition stability is influenced by varying female quality should additionally depend on interactions with other social factors, including the size and sex ratio of a population. Further, we show that although males of lower rank tend to form larger coalitions, this trend is little modulated by variation in female quality. Finally, we parameterised our model to reflect the social environment of baboon and dolphin populations and present predictions on coalition dynamics that are broadly consistent with observed data from these species. Altogether, the results of this study suggest that variation in female quality is an important modulator of coalition formation and provide a number of testable predictions to guide future empirical work.

5.5.1 General Findings

Coalition size

In this study, the prediction that high variance in female quality should lead to the formation of larger coalitions was met. Previous work has shown that resource quality is a broad predictor of the intensity of competition (Arnott and Elwood 2009). Here, we extend these findings to coalition

formation, demonstrating that the benefits to males of increased competitiveness through coalition membership outweigh the cost of sharing mating opportunities when variance in female quality is high. In our model, the range in the average size of coalitions was between 1 and 6, with the largest coalitions arising in male biased populations with high variance in female quality. In the mammalian species we reviewed, the majority of populations contained an even or female biased adult sex ratio and coalitions within these often comprised 2 or 3 individuals (see **Table 5.1**). Comparing these empirical data with our model predictions, we suggest that the formation of coalitions within these populations results from high variance in female quality (e.g. resulting from food scarcity; Simmons and Bailey 1990) and/or a sex ratio that is more male biased (e.g. resulting from short or synchronous periods of female receptivity; Emlen and Oring 1977). Testing these predictions requires more consistent recording of these social parameters, especially variance in female quality, across species, and across populations within species where coalition sizes vary (e.g. dolphins, Connor, Smolker *et al.* 1992, Möller, Beheregaray *et al.* 2001, Wiszniewski, Corrigan *et al.* 2012, Nishita, Shirakihara *et al.* 2017).

The introduction of variance in female quality also increased the variance in average coalition sizes emerging across simulations over a broad range of social parameters values. This is possibly because variation in female quality led to alternative strategies through which males could attempt to maximise their reproductive payoffs. For example, by remaining alone or in smaller, less competitive coalitions, males secure lower quality mates but are able to take a greater share of mating opportunities, which may result in similar reproductive payoffs as those obtained by males in more competitive coalitions where access to mating with higher-quality females is more restricted. In the golden orb-webbed spider (*Nephila plumipes*), males choose competitive environments that balance female quality (fecundity) and competition (Jordan, Kokko *et al.* 2014).

The results of our study suggest that variance in female quality encourages males to make similar strategic decisions in the context of coalition formation. More generally, our study highlights the role of variance in female quality as a potential driver of the evolution of alternative mating tactics in males, including cooperation with other males (Edward and Chapman 2011).

Coalition stability

In this study, we predicted high variance in female quality would increase coalition instability if intense competition for high quality females leads to males being more likely to join, merge or leave coalitions to maximise their reproductive success. In line with this prediction, coalitions were less stable across time steps when female quality was variable, though the extent of this effect depended on additional social parameters. Indeed, the effect of varying female quality on coalition stability was more apparent when males varied in their competitive abilities. This may have been because coalitions were increasingly beneficial for males in the presence of highly competitive rivals; and because variation in competitive ability provided multiple opportunities for coalition formation. This result extends previous theoretical predictions by Whitehead and Connor (2005) – who showed coalitions were more unstable when male competitive abilities varied - and indicates the combined importance of (reproductive) trait variation across both sexes in influencing the stability of male coalitions.

In our study, coalitions were also less stable under varying female quality when reproductive payoffs were more equally shared among males of a coalition. When reproductive payoffs within coalitions were highly skewed (e.g. by 99% towards the dominant male), we saw more stable coalitions. In natural systems, reduced instability under a high reproductive skew may occur if males only incur net benefits from switching or joining coalitions if they become dominant within

their new coalition group. This may result, for example, if changing coalition membership incurs costs (e.g. increased disease transmission) (Whitehead and Connor 2005). In our study, such costs were not considered, though lower instability under high reproductive skew may have occurred if males' attempts to join coalitions were more often rejected, preventing instability from the merging or formation of new coalitions. Males in our model were rejected from joining a coalition if this led to a reduced payoff for the majority of prospective partners. Thus, the effect of variance in female quality on coalition instability may be restricted when high reproductive skew limits the frequency with which males can switch and join coalitions. Barbary macaques represent an attractive species in which to test this idea, since rejection of proposed coalitions is known to occur (Young, Majolo *et al.* 2014). Gathering information on reproductive skew within coalitions, and variance in female quality across populations, of barbary macaques may be useful in understanding the importance of these factors in coalition rejections. Alternatively, predictions could be tested in other species, for example by comparing the stability of coalitions between species with low (e.g. olive baboons, Bercovitch 1988), or high, reproductive skew (e.g. Colombian red howlers, *Alouatta seniculus*, Pope 1990).

In our model, only high variance in female quality was associated with unstable coalitions forming under an even sex ratio. In this (even) sex ratio, every male consorted with a female at the beginning of simulations. Instability within coalitions was therefore presumably driven by males forming coalitions to access higher-quality females than those with whom they were initially associated. In contrast, both low and high variance in female quality lowered the stability of coalitions in male biased sex ratios, where competition for females was greater. Changes to male mating behaviour in response to the combined influence of sex ratio and variation in female quality has previously been shown in bushcrickets (*Kawanaphila nartee*), where males were less likely to

reject females in male biased groups where variance in female quality was low (Kvarnemo and Simmons 1999). Our study provides another example of how male mating behaviours (here, decisions to form coalitions) are influenced by the interaction of sex ratio and varying female quality. Further, as at least some variation in female quality can be assumed for natural populations (e.g. Simmons, Llorens *et al.* 1994, Domb and Pagel 2001, Byrne and Rice 2006), we suggest that quantifying this variation may be of reduced importance for understanding the drivers of coalition stability under male biased sex ratios.

Male rank and coalition size

Across all levels of variance in female quality, male rank was not seen to influence the size of coalitions a male formed. In many species, coalitions are often formed between mid- or high-ranking males (e.g. rhesus macques, Higham and Maestripieri 2010; baboons, Noë and Sluijter 1995; and chimpanzees (*Pan troglodytes*), Duffy, Wrangham *et al.* 2007). In our study, we assumed that males form coalitions using an 'all-up' tactic, whereby two or more males form coalitions against a more powerful opponent or coalition. However, in some species, such as rhesus macaques, high-ranking males form "conservative coalitions", supporting other high-ranked opponents during disputes to discourage attacks by coalitions of subordinates (Engh, Siebert *et al.* 2005, Berman, Ionica *et al.* 2007). Changing coalition strategies by males in response to increased competition – arising for example through increased variance in female quality, as in our model – is known to occur in natural populations (van Schaik, Pandit *et al.* 2004). Incorporating such changes into future iterations of our model may elucidate trends between male rank and coalition size by allowing high-ranking males to actively prevent coalition formation among subordinates. This may, for instance, lead to larger coalitions being formed by high-ranking males when variance in female quality is high as these (high-ranking) males benefit more by forming coalitions to

exclude low-ranking males from 'top' females than by remaining alone to access lower quality females uncontested.

5.5.2 Case studies

We tested the applicability of our model for understanding coalition formation in mammals by parameterising simulations with data from natural populations of dolphins and baboons. Overall, predictions by our model were partially consistent with observed data, and we discuss reasons for discrepancies below.

Within simulated dolphin populations, around 40% of males did not form coalitions, with the average coalition containing 1.74 males. In reality, coalitions are likely to be larger, since males within coalitions enjoy substantially greater reproductive success than solitary males (Krützen, Barré *et al.* 2004). Why then might our model predict that dolphins should form small coalitions? The inclusion of variance in female quality in our model is unlikely to be responsible for this result, since this resulted in the formation of larger (rather than smaller) coalitions in our general model. Instead, this underestimate may occur from the assumption in our model that the strength of coalitions is equal to the summed competitive ability of members (see also Whitehead and Connor 2005). While this may realistically estimate the competitive strength of coalitions for some species (e.g. barbary macaques, Bissonnette, de Vries *et al.* 2009), the monopolisation of mates by an individual male may be considerably more difficult in a three-dimensional (aquatic) environment (Möller, Beheregaray *et al.* 2001). As such, coalition formation in dolphins may confer additional benefits not accounted for by our model. Further, we parameterised simulations based on the adult sex ratio (13 females, 16 males) reported for the focal population (Smolker, Richards *et al.* 1992). However, the presence of unreceptive (pregnant females or those with young calves) may mean

the operational sex ratio of this population is more male biased (Connor, Richards *et al.* 1996). As the general results of our present study predict the emergence of larger coalitions under an increasingly male biased sex ratio, gathering and incorporating more detailed estimates on the operational sex ratio of dolphins will be useful for more accurate predictions of coalition size. To our knowledge, no information on the relationship between male rank and coalition size in dolphins currently exists (indeed, little is known about dominance relationships in dolphins generally, but see Samuels and Gifford 1997, Connor and Krützen 2015). The prediction that lower-ranked males are more frequently alone thus stands out as a prediction for future testing. This may require the refinement of methods (e.g. combining spatial tracking with behavioural observations) for estimating dominance hierarchies in an aquatic species where fine-scale measures of behaviour can be difficult.

Natural baboon populations often contain, in addition to lone males, coalitions of 2 to 3 members (Noë and Sluijter 1995). In our model, predicted coalition sizes ranged from an averaged median of 1 (all males alone) to 3.7 members. Coalitions with an averaged median exceeding 3 members were only predicted for highly male biased populations (8-9 males and 2-3 females in oestrus). As coalitions were simulated according to separately reported ranges of *n* males and *n* females, it is unclear whether populations ever contain such an extreme male bias (and thus whether these predictions are relevant). Further clarification on the average operational sex ratio (males:oestrus females) in natural populations will help clarify whether our model provides an accurate prediction of coalition size. Baboon coalitions were additionally predicted to be highly stable (mean stability 0.96). In reality, coalitions may be less stable, as data on natural baboon coalitions shows individual males are often associated with multiple, distinct coalition partners (Noë and Sluijter 1995). We further predicted high-ranking males should form smaller coalitions on average than

low- and mid-ranking males. In natural populations, coalitions often comprise mid-ranking males, as low-ranking males are frequently rejected as coalition partners and high-ranking males do not require coalition membership to secure mates (Noë and Sluijter 1995). Within our model, there is often little cost to coalition members of low-ranking males joining coalitions if this increases the coalitions' competitive ability and reproduction is skewed away from this (subordinate) male. In reality, the addition of new members into a coalition may impose costs (e.g. coordination costs; Pandit and van Schaik 2003) that reduce the payoff of current coalition members to a greater extent. Incorporating such costs into future modelling work may lead to more accurate predictions on the relationship between male rank and coalition size.

5.5.3 Incorporating relatedness

To limit the complexity of our model, we did not include variation in relatedness among males. Relatedness may be expected to influence males' decisions to join coalitions if males cooperating with kin receive indirect benefits (Hamilton 1964). For example, when mating opportunities within a coalition are highly skewed towards the dominant male, a subordinate relative may gain substantial indirect benefits from joining this coalition even if he is unlikely to gain direct access to the consorted female himself. Thus, the benefits of aiding kin during coalition formation may depend on social factors, including reproductive skew. Indeed, the dependence on social factors of kin selection in coalition formation has been indicated previously in theoretical models. For instance, (Broom, Koenig *et al.* 2009) showed coalitions were more likely to form when there was increased variance in relatedness in a group. Additionally, Whitehead and Connor (2005) showed that males consistently formed coalitions with kin only when males in the population outnumbered females by at least 2.5 to 1. In natural populations, the effect of kinship on coalition formation is

variable, with relatedness predicting patterns of coalition formation in some species (Pope 1990, Widdig, Streich *et al.* 2000) but not others (Packer 1977, Feh 1999). In this study, the species we selected to parameterise our model (dolphins and baboons) show little reported evidence that relatedness alters patterns of coalition formation (dolphins: Möller, Beheregaray *et al.* 2001, Gerber, Wittwer *et al.* 2021, Gerber, Connor *et al.* 2022, though see Parsons, Durban *et al.* 2003; baboons: Packer 1977). Applying a kin-structure to populations in future iterations of our model may allow us to predict the effects of varying female quality in species, such as Colombian red howlers, where relatedness is known to influence coalition formation (Pope 1990).

5.6 Conclusion

In this study, we investigated the influence of variation in female quality – alongside other social factors – on patterns of coalition formation. Overall, we showed that introducing variance in female quality generated larger, less stable coalitions, though the magnitude of these changes depended on other social factors, including sex ratio and population size. Together, these results suggest that incorporating variation in female quality is important to achieve a better understanding of the conditions under which coalition formation is adaptive. Additionally, we showed that parameterising our model with species data for dolphins and baboons allowed us to make partially accurate predictions on the size and stability of coalitions that should emerge in these respective populations. In a biologically relevant setting, the reproductive success of males should not only depend on competitive strategies (including coalition formation), but also decisions by females over with whom to mate. Future work may build on our findings by incorporating female preference alongside variance in quality, further elucidating the interplay between the sexes in governing decisions to cooperatively compete.

5.7 Appendix C: Supplementary Material for Chapter 5

Table C.1: Summarising information on coalition structure for populations of *Tursiops aduncus*.

Population	*n* adult males	Variance in male competitive ability	*n* adult females	Variance in female fecundity	Coalition size range	Reproductive skew within coalition
Shark Bay, Australia	Mean 16 Smolker, Richards *et al.* 1992	Mean 202.9 ± 4.16cm (SD) body length van Aswegen, Christiansen *et al.* 2019	Mean 13 Smolker, Richards *et al.* 1992	Mean 0.13 ± 0.07 (SD) calves *per* year [1]	2-3 Connor, Smolker *et al.* 1992	80% Krützen, Barré *et al.* 2004
Port Stephens, Australia	54 Wiszniewski, Beheregaray *et al.* 2010	Unreported	30 Wiszniewski, Beheregaray *et al.* 2010	Unreported	2-4 Möller, Beheregaray *et al.* 2001, Wiszniewski, Corrigan *et al.* 2012	Even Wiszniewski, Corrigan *et al.* 2012
Great Abaco Island, Bahamas	29 Parsons, Durban *et al.* 2003	Unreported	Unreported	Unreported	2 Parsons, Durban *et al.* 2003	Unreported
Amakusa, Japan	31 Nishita, Shirakihara *et al.* 2017	Unreported	Unreported	Unreported	2 Nishita, Shirakihara *et al.* 2017	Unreported
South Western Australia	Unreported	Mean 202.9 ± 1.25cm body length van Aswegen, Christiansen *et al.* 2019	Unreported	Unreported	Unreported	Unreported

[1] Information on female fecundity taken from: https://www.monkeymiadolphins.org/family-trees-2/.

Table C.2: Summarising information on coalition structure for populations of *Papio cynocephalus* and *Papio anbuis*.

Species	Population	*n* adult males	Variance in male competitive ability	*n* adult females	Variance in female fecundity	Coalition size range	Reproductive skew within coalition
cynocephalus	**HOOK, Amboseli**	6-7 Noë and Sluijter 1995	Mean 10 ± 3.9 (SD) David's Score Hausfater 1975	18-19[1] Noë and Sluijter 1995	Mean 6.43 ± 0.95 (SD) cycles since last pregnancy Fitzpatrick, Altmann *et al.* 2015 [2]	2-3 Noë and Sluijter 1995	85% to alpha Noë 1990
cynocephalus	**ALTO, Amboseli**	6-9 Noë and Sluijter 1995	Unreported	14-16 Noë and Sluijter 1995		2-3 Noë and Sluijter 1995	Unreported
anubis	**Gilgil, Kenya**	4-8 Bercovitch 1988	Unreported	18-20 Bercovitch 1988	Unreported	2-3 Bercovitch 1988	Equal Bercovitch 1988
anubis	**Gombe, Tanzania**	Unreported	Unreported	Unreported	Mean 18.98 ± 0.34cm sexual swelling width Domb 2000	Unreported	Unreported

[1] 2-7 females in synchronous oestrus. [2] Data from 'Amboseli population'.

Table C.3: Summary statistics for averaged values of median coalition size (±SE) and stability (±SE) across 100-time steps for 20 simulations *per* combination of social parameters. Columns 5-10 indicate respective summary statistics of stability and coalition size for populations containing 6, 12 or 24 males.

Sex Ratio	Reproductive Skew	Male Variance	Female Variance	Coalition Size ± SE			Stability ± SE		
				6	12	24	6	12	24
6:1	Equal	0.0	0.0	2.850 ± 0.014	1.500 ± 0.000	1.500 ± 0.000	0.968 ± 0.001	0.990 ± 0.000	0.990 ± 0.000
			0.1	*NA*	1.648 ± 0.052	1.549 ± 0.034	*NA*	0.988 ± 0.001	0.988 ± 0.001
			0.5	*NA*	1.771 ± 0.056	1.647 ± 0.080	*NA*	0.986 ± 0.002	0.986 ± 0.002
		0.1	0.0	2.948 ± 0.019	3.883 ± 0.047	4.395 ± 0.033	0.982 ± 0.002	0.922 ± 0.033	0.922 ± 0.033
			0.1	*NA*	4.131 ± 0.235	4.504 ± 0.262	*NA*	0.952 ± 0.006	0.952 ± 0.006
			0.5	*NA*	5.225 ± 0.232	5.543 ± 0.239	*NA*	0.946 ± 0.006	0.946 ± 0.006
		0.5	0.0	2.891 ± 0.050	3.181 ± 0.158	3.366 ± 0.181	0.971 ± 0.009	0.923 ± 0.030	0.923 ± 0.030
			0.1	*NA*	3.495 ± 0.226	2.565 ± 0.136	*NA*	0.900 ± 0.046	0.900 ± 0.046
			0.5	*NA*	3.695 ± 0.308	3.605 ± 0.333	*NA*	0.917 ± 0.015	0.917 ± 0.015
	0.5	0.0	0.0	2.900 ± 0.013	1.500 ± 0.000	1.500 ± 0.000	0.996 ± 0.001	1.000 ± 0.000	1.000 ± 0.000
			0.1	*NA*	1.998 ± 0.000	2.606 ± 0.145	*NA*	1.000 ± 0.001	1.000 ± 0.001
			0.5	*NA*	1.972 ± 0.025	2.365 ± 0.111	*NA*	1.000 ± 0.001	1.000 ± 0.001
		0.1	0.0	2.977 ± 0.007	3.950 ± 0.006	4.445 ± 0.006	0.994 ± 0.002	0.991 ± 0.002	0.991 ± 0.002
			0.1	*NA*	4.896 ± 0.241	5.265 ± 0.152	*NA*	0.919 ± 0.019	0.919 ± 0.019
			0.5	*NA*	5.360 ± 0.215	6.153 ± 0.256	*NA*	0.895 ± 0.025	0.895 ± 0.025
		0.5	0.0	2.853 ± 0.068	3.078 ± 0.119	4.439 ± 0.086	0.994 ± 0.002	0.988 ± 0.002	0.988 ± 0.002
			0.1	*NA*	3.880 ± 0.234	4.697 ± 0.213	*NA*	0.949 ± 0.017	0.949 ± 0.017
			0.5	*NA*	4.310 ± 0.276	4.745 ± 0.191	*NA*	0.880 ± 0.024	0.880 ± 0.024
	0.75	0.0	0.0	2.884 ± 0.014	1.500 ± 0.000	1.500 ± 0.000	0.995 ± 0.001	0.999 ± 0.001	0.999 ± 0.001
			0.1	*NA*	1.922 ± 0.041	1.964 ± 0.113	*NA*	0.998 ± 0.001	0.998 ± 0.001
			0.5	*NA*	1.921 ± 0.041	2.041 ± 0.093	*NA*	0.998 ± 0.001	0.998 ± 0.001
		0.1	0.0	2.966 ± 0.008	3.888 ± 0.047	4.431 ± 0.005	0.994 ± 0.002	0.992 ± 0.002	0.992 ± 0.002
			0.1	*NA*	5.372 ± 0.234	5.511 ± 0.194	*NA*	0.950 ± 0.014	0.950 ± 0.014
			0.5	*NA*	5.477 ± 0.165	6.045 ± 0.298	*NA*	0.854 ± 0.029	0.854 ± 0.029
		0.5	0.0	2.882 ± 0.050	3.594 ± 0.125	4.412 ± 0.089	0.996 ± 0.001	0.994 ± 0.001	0.994 ± 0.001
			0.1	*NA*	4.494 ± 0.262	4.967 ± 0.171	*NA*	0.959 ± 0.009	0.959 ± 0.009

			0.5	*NA*	4.504 ± 0.269	5.005 ± 0.109	*NA*	0.891 ± 0.019	0.891 ± 0.019
	0.99	**0.0**	**0.0**	2.891 ± 0.015	1.500 ± 0.000	1.500 ± 0.000	0.996 ± 0.001	1.000 ± 0.001	1.000 ± 0.001
			0.1	*NA*	1.945 ± 0.034	1.974 ± 0.084	*NA*	1.000 ± 0.001	1.000 ± 0.001
			0.5	*NA*	1.971 ± 0.025	2.010 ± 0.100	*NA*	1.000 ± 0.001	1.000 ± 0.001
		0.1	**0.0**	2.969 ± 0.008	3.884 ± 0.048	4.454 ± 0.004	0.991 ± 0.001	0.994 ± 0.002	0.994 ± 0.002
			0.1	*NA*	4.914 ± 0.235	5.943 ± 0.140	*NA*	0.954 ± 0.014	0.954 ± 0.014
			0.5	*NA*	5.550 ± 0.159	5.709 ± 0.114	*NA*	0.875 ± 0.025	0.875 ± 0.025
		0.5	**0.0**	2.919 ± 0.014	3.436 ± 0.145	4.282 ± 0.068	0.994 ± 0.002	0.991 ± 0.002	0.991 ± 0.002
			0.1	*NA*	4.099 ± 0.258	4.821 ± 0.301	*NA*	0.970 ± 0.014	0.970 ± 0.014
			0.5	*NA*	4.011 ± 0.269	5.179 ± 0.172	*NA*	0.905 ± 0.020	0.905 ± 0.020
3:1	**Equal**	**0.0**	**0.0**	1.500 ± 0.000	1.500 ± 0.000	1.500 ± 0.000	0.988 ± 0.001	0.990 ± 0.000	0.990 ± 0.000
			0.1	1.549 ± 0.034	1.500 ± 0.000	1.500 ± 0.000	0.987 ± 0.002	0.990 ± 0.000	0.990 ± 0.000
			0.5	1.844 ± 0.052	1.599 ± 0.045	1.525 ± 0.025	0.979 ± 0.002	0.989 ± 0.001	0.989 ± 0.001
		0.1	**0.0**	1.992 ± 0.001	2.488 ± 0.002	2.462 ± 0.024	0.982 ± 0.001	0.957 ± 0.003	0.957 ± 0.003
			0.1	2.088 ± 0.065	2.393 ± 0.068	1.940 ± 0.074	0.981 ± 0.003	0.700 ± 0.062	0.700 ± 0.062
			0.5	2.545 ± 0.117	3.211 ± 0.227	3.025 ± 0.175	0.978 ± 0.005	0.652 ± 0.069	0.652 ± 0.069
		0.5	**0.0**	1.741 ± 0.076	2.229 ± 0.092	2.034 ± 0.056	0.978 ± 0.007	0.940 ± 0.006	0.940 ± 0.006
			0.1	1.670 ± 0.088	1.499 ± 0.059	1.524 ± 0.021	0.891 ± 0.059	0.424 ± 0.055	0.424 ± 0.055
			0.5	1.676 ± 0.062	2.159 ± 0.155	1.995 ± 0.077	0.855 ± 0.061	0.615 ± 0.079	0.615 ± 0.079
	0.5	**0.0**	**0.0**	1.500 ± 0.000	1.500 ± 0.000	1.500 ± 0.000	0.998 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
			0.1	1.599 ± 0.045	2.095 ± 0.057	2.194 ± 0.079	1.000 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
			0.5	1.772 ± 0.057	2.071 ± 0.053	2.437 ± 0.129	0.998 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
		0.1	**0.0**	1.996 ± 0.001	2.490 ± 0.001	2.494 ± 0.011	0.996 ± 0.001	0.992 ± 0.002	0.992 ± 0.002
			0.1	2.103 ± 0.034	2.683 ± 0.047	2.937 ± 0.061	0.887 ± 0.038	0.936 ± 0.010	0.936 ± 0.010
			0.5	2.453 ± 0.104	2.944 ± 0.104	3.372 ± 0.074	0.913 ± 0.039	0.735 ± 0.037	0.735 ± 0.037
		0.5	**0.0**	1.818 ± 0.065	2.359 ± 0.057	2.485 ± 0.070	0.983 ± 0.015	0.990 ± 0.003	0.990 ± 0.003
			0.1	1.875 ± 0.106	2.422 ± 0.187	3.117 ± 0.197	0.917 ± 0.030	0.949 ± 0.011	0.949 ± 0.011
			0.5	2.030 ± 0.131	2.533 ± 0.159	2.937 ± 0.081	0.970 ± 0.008	0.836 ± 0.032	0.836 ± 0.032
	0.75	**0.0**	**0.0**	1.500 ± 0.000	1.500 ± 0.000	1.500 ± 0.000	0.997 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
			0.1	1.525 ± 0.025	2.007 ± 0.078	1.833 ± 0.081	0.998 ± 0.001	0.998 ± 0.002	0.998 ± 0.002
			0.5	1.673 ± 0.054	2.117 ± 0.110	1.887 ± 0.080	0.998 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
		0.1	**0.0**	1.979 ± 0.003	2.479 ± 0.003	2.482 ± 0.003	0.990 ± 0.002	0.990 ± 0.002	0.990 ± 0.002

			0.1	2.340 ± 0.107	2.743 ± 0.059	3.303 ± 0.085	0.968 ± 0.008	0.989 ± 0.003	0.989 ± 0.003
			0.5	2.579 ± 0.108	2.813 ± 0.083	3.269 ± 0.060	0.990 ± 0.003	0.884 ± 0.020	0.884 ± 0.020
		0.5	**0.0**	1.813 ± 0.064	2.355 ± 0.060	2.500 ± 0.067	0.996 ± 0.002	0.988 ± 0.002	0.988 ± 0.002
			0.1	1.813 ± 0.102	2.678 ± 0.079	3.124 ± 0.099	0.959 ± 0.023	0.980 ± 0.006	0.980 ± 0.006
			0.5	2.275 ± 0.123	2.782 ± 0.093	3.205 ± 0.078	0.950 ± 0.021	0.894 ± 0.019	0.894 ± 0.019
	0.99	**0.0**	**0.0**	1.500 ± 0.000	1.500 ± 0.000	1.500 ± 0.000	0.999 ± 0.001	0.996 ± 0.002	0.996 ± 0.002
			0.1	1.575 ± 0.041	1.946 ± 0.034	1.901 ± 0.088	0.999 ± 0.001	0.999 ± 0.001	0.999 ± 0.001
			0.5	1.623 ± 0.049	1.846 ± 0.052	1.982 ± 0.120	0.998 ± 0.001	0.998 ± 0.001	0.998 ± 0.001
		0.1	**0.0**	1.987 ± 0.003	2.477 ± 0.002	2.489 ± 0.003	0.995 ± 0.001	0.990 ± 0.002	0.990 ± 0.002
			0.1	2.763 ± 0.090	2.920 ± 0.034	3.357 ± 0.112	0.993 ± 0.002	0.988 ± 0.002	0.988 ± 0.002
			0.5	2.814 ± 0.079	2.835 ± 0.053	3.130 ± 0.111	0.992 ± 0.002	0.969 ± 0.005	0.969 ± 0.005
		0.5	**0.0**	1.896 ± 0.035	2.376 ± 0.043	2.507 ± 0.062	0.907 ± 0.037	0.980 ± 0.006	0.980 ± 0.006
			0.1	2.308 ± 0.134	2.766 ± 0.063	2.965 ± 0.112	0.972 ± 0.019	0.985 ± 0.003	0.985 ± 0.003
			0.5	2.274 ± 0.106	2.596 ± 0.078	3.310 ± 0.118	0.957 ± 0.024	0.950 ± 0.014	0.950 ± 0.014
1:1	**Equal**	**0.0**	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.050 ± 0.034	1.048 ± 0.033	1.252 ± 0.054	0.999 ± 0.001	0.994 ± 0.001	0.994 ± 0.001
			0.5	1.349 ± 0.052	1.499 ± 0.001	1.500 ± 0.000	0.992 ± 0.002	0.968 ± 0.003	0.968 ± 0.003
		0.1	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.240 ± 0.055	1.452 ± 0.035	1.499 ± 0.000	0.891 ± 0.054	0.805 ± 0.031	0.805 ± 0.031
		0.5	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.5	**0.0**	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.049 ± 0.034	1.245 ± 0.056	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.284 ± 0.060	1.618 ± 0.042	1.956 ± 0.026	0.986 ± 0.012	0.984 ± 0.005	0.984 ± 0.005
		0.1	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.403 ± 0.057	1.795 ± 0.057	2.426 ± 0.110	0.917 ± 0.039	0.982 ± 0.005	0.982 ± 0.005
		0.5	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000

			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.0	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.350 ± 0.053	1.524 ± 0.044	1.616 ± 0.058	1.000 ± 0.000	0.999 ± 0.001	0.999 ± 0.001
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.75	**0.1**	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.348 ± 0.052	1.476 ± 0.065	1.803 ± 0.072	0.945 ± 0.027	0.983 ± 0.008	0.983 ± 0.008
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.0	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.99	**0.1**	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.0	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.025 ± 0.025	1.099 ± 0.046	1.123 ± 0.049	1.000 ± 0.001	0.994 ± 0.003	0.994 ± 0.003
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	Equal	**0.1**	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.099 ± 0.045	1.074 ± 0.040	1.024 ± 0.024	0.995 ± 0.004	1.000 ± 0.001	1.000 ± 0.001
1:2			**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.021 ± 0.021	1.000 ± 0.000	1.000 ± 0.000	0.953 ± 0.047	1.000 ± 0.000	1.000 ± 0.000
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.0	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.5		**0.5**	1.000 ± 0.000	1.097 ± 0.045	1.179 ± 0.056	1.000 ± 0.000	0.996 ± 0.004	0.996 ± 0.004
			0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.1	**0.1**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000

			0.5	1.049 ± 0.034	1.080 ± 0.044	1.024 ± 0.024	0.998 ± 0.002	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.024 ± 0.024	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.75	**0.0**	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.1	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.99	**0.0**	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.1	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	**0.0**	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000

Table C.4: Summary statistics for averaged coalition sizes (±SE) of 'low', 'mid' and 'high' ranking males across 100-time steps for 20 simulations *per* combination of social parameters. Columns 6-10 indicate respective summary statistics of stability and coalition size for populations containing 6, 12 or 24 males. Within each simulation, ranks were assigned to each male depending on whether their competitive ability was in the lowest ('low'), middle ('mid') or highest ('high') tercile of the population.

Sex Ratio	Skew	Male Variance	Female Variance	6 males			12 males			24 males		
				Low	Mid	High	Low	Mid	High	Low	Mid	High
6:1	Equal	0.1	0.0	2.963 ± 0.014	2.977 ± 0.007	2.982 ± 0.007	3.872 ± 0.072	3.935 ± 0.025	3.935± 0.025	4.545 ± 0.053	4.460 ± 0.033	4.467 ± 0.004
			0.1	*NA*	*NA*	*NA*	4.237 ± 0.226	4.247 ± 0.233	4.453 ± 0.204	4.530 ± 0.264	4.734 ± 0.225	4.905 ± 0.222
			0.5	*NA*	*NA*	*NA*	5.167 ± 0.266	5.369 ± 0.219	5.472 ± 0.168	6.235 ± 0.324	6.045 ± 0.370	5.698 ± 0.317
		0.5	0.0	3.055 ± 0.093	2.996 ± 0.074	2.873 ± 0.067	3.139 ± 0.177	3.582 ± 0.135	3.498 ± 0.097	3.364 ± 0.195	3.720 ± 0.158	3.810 ± 0.148
			0.1	*NA*	*NA*	*NA*	3.303 ± 0.244	3.990 ± 0.213	4.058 ± 0.199	2.359 ± 0.160	2.884 ± 0.185	3.229 ± 0.156
			0.5	*NA*	*NA*	*NA*	3.530 ± 0.340	4.311 ± 0.293	4.418 ± 0.277	3.318 ± 0.370	4.212 ± 0.359	4.462 ± 0.325
	0.5	0.1	0.0	2.987 ± 0.006	2.993 ± 0.003	2.989 ± 0.003	3.964 ± 0.006	3.969 ± 0.004	3.967 ± 0.006	4.541 ± 0.039	4.524 ± 0.035	4.455 ± 0.005
			0.1	*NA*	*NA*	*NA*	5.067 ± 0.268	5.010 ± 0.227	5.105 ± 0.213	5.778 ± 0.276	5.889 ± 0.246	5.585 ± 0.202
			0.5	*NA*	*NA*	*NA*	5.344 ± 0.242	5.682 ± 0.255	5.556 ± 0.156	7.101 ± 0.331	7.019 ± 0.309	6.387 ± 0.259
		0.5	0.0	2.912 ± 0.087	2.879 ± 0.068	2.877 ± 0.068	2.983 ± 0.146	3.554 ± 0.102	3.504 ± 0.074	4.560 ± 0.107	4.641 ± 0.061	4.575 ± 0.058
			0.1	*NA*	*NA*	*NA*	3.589 ± 0.336	4.472 ± 0.220	4.506 ± 0.225	5.099 ± 0.228	5.594 ± 0.241	5.304 ± 0.147
			0.5	*NA*	*NA*	*NA*	4.050 ± 0.356	4.796 ± 0.258	5.000 ± 0.188	5.505 ± 0.200	5.927 ± 0.287	5.307 ± 0.212
	0.75	0.1	0.0	2.988 ± 0.006	3.035 ± 0.049	2.980 ± 0.005	3.908 ± 0.048	3.931 ± 0.023	3.926 ± 0.024	4.513 ± 0.035	4.489 ± 0.026	4.442 ± 0.005
			0.1	*NA*	*NA*	*NA*	5.867 ± 0.292	5.556 ± 0.254	5.507 ± 0.183	6.201 ± 0.353	6.137 ± 0.376	6.101 ± 0.287
			0.5	*NA*	*NA*	*NA*	5.644 ± 0.198	5.627 ± 0.201	5.612 ± 0.139	6.765 ± 0.260	6.863 ± 0.285	6.493 ± 0.294
		0.5	0.0	2.933 ± 0.060	2.980 ± 0.072	2.917 ± 0.049	3.652 ± 0.137	3.768 ± 0.109	3.789 ± 0.063	4.512 ± 0.063	4.661 ± 0.064	4.525 ± 0.063
			0.1	*NA*	*NA*	*NA*	4.552 ± 0.278	5.246 ± 0.181	5.145 ± 0.199	5.581 ± 0.256	5.446 ± 0.187	5.376 ± 0.209
			0.5	*NA*	*NA*	*NA*	4.214 ± 0.363	5.008 ± 0.242	5.058 ± 0.210	6.101 ± 0.303	5.927 ± 0.198	5.931 ± 0.280
	0.99	0.1	0.0	2.988 ± 0.005	3.037 ± 0.049	2.978 ± 0.005	3.912 ± 0.049	3.951 ± 0.007	3.922 ± 0.025	4.537 ± 0.038	4.482 ± 0.017	4.458 ± 0.005
			0.1	*NA*	*NA*	*NA*	5.208 ± 0.327	4.966 ± 0.238	5.051 ± 0.234	6.438 ± 0.229	6.323 ± 0.162	6.327 ± 0.191
			0.5	*NA*	*NA*	*NA*	5.763 ± 0.224	5.670 ± 0.133	5.693 ± 0.119	7.005 ± 0.256	6.690 ± 0.190	6.594 ± 0.204

		0.5	0.0	3.035 ± 0.071	2.974 ± 0.005	2.966 ± 0.005	3.341 ± 0.203	3.743 ± 0.125	3.657 ± 0.101	4.320 ± 0.094	4.559 ± 0.052	4.453 ± 0.031
			0.1	*NA*	*NA*	*NA*	3.956 ± 0.338	4.660 ± 0.242	4.763 ± 0.194	5.324 ± 0.305	5.589 ± 0.299	5.442 ± 0.292
			0.5	*NA*	*NA*	*NA*	3.885 ± 0.371	4.709 ± 0.259	4.726 ± 0.229	6.145 ± 0.251	6.144 ± 0.250	5.720 ± 0.193
3:1	Equal	0.1	0.0	1.996 ± 0.002	1.997 ± 0.001	1.992 ± 0.001	2.631 ± 0.049	2.516 ± 0.043	2.343 ± 0.052	2.733 ± 0.062	2.583 ± 0.042	2.493 ± 0.001
			0.1	2.090 ± 0.065	2.091 ± 0.065	2.090 ± 0.066	2.336 ± 0.077	2.561 ± 0.057	2.449 ± 0.061	1.871 ± 0.095	2.055 ± 0.087	2.050 ± 0.090
			0.5	2.524 ± 0.131	2.578 ± 0.109	2.526 ± 0.131	3.453 ± 0.258	3.557 ± 0.262	3.261 ± 0.218	3.135 ± 0.197	3.469 ± 0.180	3.195 ± 0.183
		0.5	0.0	1.784 ± 0.101	2.020 ± 0.104	1.644 ± 0.081	2.324 ± 0.108	2.305 ± 0.090	2.244 ± 0.091	2.073 ± 0.075	2.392 ± 0.054	2.364 ± 0.067
			0.1	1.524 ± 0.102	1.853 ± 0.116	1.626 ± 0.100	1.316 ± 0.058	1.626 ± 0.085	1.528 ± 0.076	1.238 ± 0.049	1.517 ± 0.019	1.477 ± 0.031
			0.5	1.532 ± 0.093	1.970 ± 0.055	1.800 ± 0.107	1.908 ± 0.159	2.552 ± 0.201	2.504 ± 0.201	1.703 ± 0.084	2.097 ± 0.120	2.318 ± 0.125
	0.5	0.1	0.0	1.999 ± 0.001	1.999 ± 0.001	1.996 ± 0.001	2.495 ± 0.001	2.518 ± 0.023	2.417 ± 0.041	2.703 ± 0.053	2.546 ± 0.028	2.493 ± 0.010
			0.1	2.274 ± 0.078	2.195 ± 0.068	2.101 ± 0.037	2.889 ± 0.108	3.009 ± 0.109	2.647 ± 0.063	3.123 ± 0.084	3.193 ± 0.084	2.795 ± 0.093
			0.5	2.496 ± 0.112	2.557 ± 0.103	2.481 ± 0.102	3.369 ± 0.134	3.149 ± 0.144	3.217 ± 0.098	3.722 ± 0.098	3.610 ± 0.113	3.760 ± 0.107
		0.5	0.0	1.894 ± 0.093	2.019 ± 0.076	1.768 ± 0.067	2.460 ± 0.073	2.475 ± 0.075	2.377 ± 0.044	2.588 ± 0.089	2.525 ± 0.024	2.588 ± 0.043
			0.1	1.922 ± 0.115	2.206 ± 0.199	1.862 ± 0.108	2.495 ± 0.256	2.754 ± 0.240	2.293 ± 0.193	3.486 ± 0.200	3.545 ± 0.186	3.026 ± 0.204
			0.5	2.064 ± 0.166	2.332 ± 0.161	2.056 ± 0.142	2.698 ± 0.203	2.801 ± 0.189	2.799 ± 0.186	3.255 ± 0.129	3.290 ± 0.129	3.177 ± 0.138
	0.75	0.1	0.0	2.049 ± 0.044	2.002 ± 0.002	1.975 ± 0.003	2.539 ± 0.031	2.549 ± 0.036	2.381 ± 0.046	2.601 ± 0.043	2.528 ± 0.030	2.484 ± 0.003
			0.1	2.581 ± 0.175	2.776 ± 0.180	2.185 ± 0.092	3.109 ± 0.114	2.805 ± 0.101	2.758 ± 0.069	3.462 ± 0.055	3.317 ± 0.097	3.212 ± 0.091
			0.5	2.842 ± 0.142	2.782 ± 0.147	2.433 ± 0.127	3.271 ± 0.132	3.227 ± 0.118	3.139 ± 0.145	3.172 ± 0.092	3.674 ± 0.080	3.845 ± 0.150
		0.5	0.0	1.848 ± 0.073	1.997 ± 0.072	1.786 ± 0.065	2.347 ± 0.083	2.490 ± 0.062	2.401 ± 0.054	2.580 ± 0.084	2.577 ± 0.038	2.567 ± 0.039
			0.1	1.944 ± 0.180	2.216 ± 0.185	1.796 ± 0.116	2.857 ± 0.123	3.240 ± 0.111	2.671 ± 0.089	3.410 ± 0.208	3.478 ± 0.113	3.013 ± 0.117
			0.5	2.254 ± 0.198	2.514 ± 0.148	2.415 ± 0.118	3.060 ± 0.171	3.178 ± 0.123	3.008 ± 0.079	3.681 ± 0.194	3.126 ± 0.112	3.637 ± 0.139
	0.99	0.1	0.0	2.005 ± 0.001	1.998 ± 0.002	1.985 ± 0.004	2.490 ± 0.002	2.549 ± 0.036	2.379 ± 0.046	2.522 ± 0.021	2.531 ± 0.029	2.486 ± 0.003
			0.1	3.153 ± 0.155	3.250 ± 0.172	2.502 ± 0.110	3.078 ± 0.083	3.101 ± 0.109	2.936 ± 0.083	3.391 ± 0.108	3.305 ± 0.115	3.318 ± 0.129
			0.5	3.272 ± 0.144	3.155 ± 0.150	2.570 ± 0.108	3.151 ± 0.090	3.191 ± 0.096	3.163 ± 0.094	3.178 ± 0.141	3.579 ± 0.277	4.311 ± 0.298
		0.5	0.0	2.077 ± 0.063	2.184 ± 0.083	1.765 ± 0.052	2.406 ± 0.052	2.523 ± 0.052	2.418 ± 0.034	2.635 ± 0.081	2.559 ± 0.033	2.544 ± 0.045
			0.1	2.594 ± 0.201	2.625 ± 0.166	2.289 ± 0.140	2.891 ± 0.110	2.970 ± 0.091	2.914 ± 0.081	2.964 ± 0.126	3.188 ± 0.108	3.207 ± 0.081
			0.5	2.389 ± 0.216	2.803 ± 0.145	2.482 ± 0.093	3.085 ± 0.166	2.977 ± 0.106	2.913 ± 0.090	3.450 ± 0.150	3.451 ± 0.173	3.678 ± 0.164
1:1	Equal	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.382 ± 0.095	1.174 ± 0.066	1.014 ± 0.007	1.446 ± 0.047	1.442 ± 0.036	1.119 ± 0.041	1.479 ± 0.015	1.511 ± 0.011	1.068 ± 0.032

		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.5	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.624 ± 0.100	1.279 ± 0.094	1.094 ± 0.048	2.024 ± 0.105	1.801 ± 0.151	1.114 ± 0.063	2.856 ± 0.120	2.474 ± 0.143	1.420 ± 0.130
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.75	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.548 ± 0.092	1.242 ± 0.059	1.126 ± 0.052	1.498 ± 0.076	1.368 ± 0.068	1.158 ± 0.052	1.828 ± 0.071	1.610 ± 0.110	1.422 ± 0.081
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.99	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
1:2	Equal	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.171 ± 0.081	1.025 ± 0.025	1.000 ± 0.000	1.096 ± 0.056	1.025 ± 0.025	1.000 ± 0.000	1.024 ± 0.024	1.000 ± 0.000	1.000 ± 0.000
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.018 ± 0.018	1.024 ± 0.024	1.016 ± 0.016	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.5	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.074 ± 0.054	1.024 ± 0.024	1.000 ± 0.000	1.112 ± 0.065	1.030 ± 0.030	1.000 ± 0.000	1.024 ± 0.024	1.000 ± 0.000	1.000 ± 0.000

		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.024 ± 0.024	1.024 ± 0.024	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.75	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	0.99	0.1	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
		0.5	0.0	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.1	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
			0.5	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000

Table C.5: Summary statistics for averaged values of stability (±SE) and median coalition size (±SE) across 100-time steps for 20 simulations *per* combination of 'n males' and 'n females'.

n males	n females	Stability (±SE)	Coalition size (±SE)
6	2	0.931 ± 0.031	2.341 ± 0.105
	3	0.907 ± 0.032	1.760 ± 0.047
	4	0.884 ± 0.041	1.509 ± 0.014
	5	0.998 ± 0.001	1.500 ± 0.000
	6	1.000 ± 0.000	1.000 ± 0.000
	7	1.000 ± 0.000	1.000 ± 0.000
7	2	0.989 ± 0.003	2.844 ± 0.138
	3	0.937 ± 0.024	2.029 ± 0.111
	4	0.960 ± 0.018	1.579 ± 0.039
	5	0.919 ± 0.027	1.470 ± 0.025
	6	1.000 ± 0.001	1.475 ± 0.025
	7	1.000 ± 0.000	1.000 ± 0.000
8	2	0.993 ± 0.002	3.188 ± 0.178
	3	0.930 ± 0.026	2.459 ± 0.113
	4	0.967 ± 0.010	1.855 ± 0.045
	5	0.946 ± 0.025	1.584 ± 0.037
	6	0.899 ± 0.032	1.477 ± 0.026
	7	0.996 ± 0.003	1.369 ± 0.049
9	2	0.992 ± 0.002	3.583 ± 0.202
	3	0.988 ± 0.002	2.683 ± 0.109
	4	0.974 ± 0.007	2.212 ± 0.071
	5	0.982 ± 0.005	1.719 ± 0.053
	6	0.941 ± 0.024	1.598 ± 0.039
	7	0.977 ± 0.010	1.473 ± 0.025

Table C.6: Summary statistics for averaged coalition sizes (±SE) of 'low', 'mid' and 'high' ranking males across 100-time steps for 20 simulations *per* combination of 'n males' and 'n females'. Within each simulation, ranks were assigned to each male depending on whether their competitive ability was in the lowest ('low'), middle ('mid') or highest ('high') tercile of the population. For populations containing 7 males, the middle tercile contained 3 males. For populations containing 8 males, the lowest and middle terciles each contained 3 males.

n males	n females	Male Rank		
		Low	Mid	High
6	2	2.654 ± 0.216	2.690 ± 0.204	2.273 ± 0.195
	3	2.064 ± 0.076	1.909 ± 0.099	1.643 ± 0.127
	4	1.895 ± 0.059	1.356 ± 0.089	1.398 ± 0.102
	5	1.625 ± 0.109	1.249 ± 0.097	1.125 ± 0.075
	6	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
	7	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
7	2	2.900 ± 0.182	2.950 ± 0.150	2.749 ± 0.207
	3	2.142 ± 0.101	2.294 ± 0.124	1.750 ± 0.114
	4	1.915 ± 0.112	1.712 ± 0.121	1.659 ± 0.113
	5	1.808 ± 0.069	1.348 ± 0.092	1.269 ± 0.092
	6	1.601 ± 0.111	1.216 ± 0.092	1.025 ± 0.035
	7	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.000
8	2	3.421 ± 0.263	3.490 ± 0.195	3.220 ± 0.235
	3	2.630 ± 0.201	2.932 ± 0.207	1.967 ± 0.109
	4	2.153 ± 0.093	2.055 ± 0.118	1.796 ± 0.101
	5	1.867 ± 0.106	1.661 ± 0.114	1.461 ± 0.117
	6	1.647 ± 0.091	1.239 ± 0.081	1.180 ± 0.073
	7	1.387 ± 0.108	1.100 ± 0.067	1.000 ± 0.000
9	2	4.044 ± 0.390	4.098 ± 0.254	4.276 ± 0.274
	3	2.877 ± 0.201	2.976 ± 0.172	2.711 ± 0.194
	4	2.322 ± 0.097	2.407 ± 0.120	2.103 ± 0.111
	5	2.156 ± 0.095	1.817 ± 0.137	1.864 ± 0.128
	6	1.945 ± 0.100	1.445 ± 0.121	1.568 ± 0.103
	7	1.660 ± 0.099	1.198 ± 0.083	1.266 ± 0.098

Chapter 6: *General Discussion*

6.1 Key Findings

Contest competition over limited resources should occur whenever the benefits of competing outweigh the costs (Darwin 1859, Darwin 1871, Hardy and Briffa 2013). When changes to the social environment (i.e. the composition of individuals within a population) alter these costs and benefits, strategic modification of competitive behaviours is predicted to occur. Despite this prediction, empirical tests on many aspects of these strategic behavioural modifications are lacking, impacting our understanding on how the social environment shapes evolutionary processes. Additionally, the importance of some features of the social environment may have been previously overlooked, and suitable theoretical frameworks are required to predict how these factors shape competitive behaviours. In this thesis, I address some of these knowledge gaps and investigate how the social environment influences a range of competitive behaviours. In Chapters 2-4, I use behavioural experiments to understand how competitive strategies (intrasexual aggression, and mating, expected to respond to the risk and intensity of sperm competition; (Parker and Ball 2005)) in male cichlids, and male and female red junglefowl, respond to changes in relevant aspects of the social environment. In Chapter 5, I use a theoretical model applicable to a range of species to illustrate the importance of variance in female quality in modulating patterns of male coalition formation.

In Chapter 2, I showed that, contrary to theoretical expectations, patterns of aggression in male cichlids (*Lamprologus ocellatus*) did not show a concave relationship with competitor density. However, with increasing stocking (competitor) density, aggression became increasingly confined

to larger fish within groups, revealing variation in how individuals respond to a changing social environment. While fishkeeping advice often extols the benefits of high stocking densities in reducing aggression, I suggest these benefits do not come from a reduction of aggression, but instead from the increasing tendency for contests to occur among those individuals most capable of bearing the costs (Maynard Smith and Brown 1986).

In Chapter 3, I explored changes in competitor density in an alternative way *via* manipulations of the sex ratio in flocks of red junglefowl (*Gallus gallus*). Further, I explored how altering individuals' perception of the social environment (through manipulations of environmental complexity) can mediate the strength of behavioural responses to a changing sex ratio. Overall, I found males showed increased intra-sexual aggression in 'even' (*vs* 'female biased' sex ratios). Additionally, I showed that two male dominance behaviours (crowing and wing flapping) responded differently to changes in sex ratio and showed opposing temporal trends, suggesting a subtle difference in their function. In contrast to the effect of sex ratio, changes to environmental complexity had little detectable influence on male competitive behaviour. In comparison, the results of our survey in Chapter 2 suggest environmental complexity is a useful complement to increased stocking density for managing aggression in cichlids (including *L. ocellatus*). Environmental complexity has additionally been shown to reduce aggression among freshwater crayfish (*Cherax destructor*) and guppies (*Poecilia reticulata*) and influence intersexual interactions, including weakening sexual conflict in *Drosophila melanogaster* (Baird, Patullo *et al.* 2006, Hibler and Houde 2006, Malek and Long 2019). Further studies may use these species for additional investigations on the interaction between environmental complexity and competitor density/sex ratio.

In Chapter 4, I explored the drivers of intra-sexual aggression in female red junglefowl by comparing flocks with different age- and sex-compositions. I found that aggression was initially higher in flocks containing five young hens ('young' flocks), compared to flocks containing four young hens and either an old hen ('old' flocks) or a male ('male' flocks). Over time, aggression decreased in 'young' flocks, remained constant in 'male' flocks and increased in 'old' flocks. I suggest that constant levels of aggression in 'male' flocks may have resulted if increased perching by females avoiding sexual harassment concomitantly delayed the establishment of the female hierarchies (by preventing escalations of intrasexual aggression). This latter finding provides an interesting comparison to Chapter 3, indicating that the presence of relatively few members of the opposite sex increases intrasexual aggression among males, but decreases intrasexual aggression among females. Lower potential reproductive rates and higher investment into parental care means intrasexual aggression over mating opportunities are less likely to arise in females, compared to males (Campbell 2004, Stockley and Bro-Jørgensen 2011, Stockley and Campbell 2013). When investigating the influence of the social environment on competitive strategies, such as aggression, it is therefore important to consider intersexual variation in the contexts within which these competitive behaviours are beneficial.

In both Chapters 3 and 4, I describe trends in competitive behaviours over time. In Chapter 3, courtship and dominance behaviours decreased over successive trial days, whereas counts of mating and aggression did not change. In Chapter 4, temporal trends of intra-sexual aggression varied depending on the flock composition. Across these two chapters, I initially predicted that the intensity of measured behaviours would decline across successive trial days; owing to increased social and sexual familiarity (Kelley, Graves *et al.* 1999, Zajitschek, Evans *et al.* 2006, Lovlie and Pizzari 2007). The fact that our findings did not always support this decline indicates the

importance of conducting studies across multiple time points in order to avoid under- or overestimating the expression of behaviours within different social environments.

In Chapter 5, I used a theoretical model to examine how the size and stability of male coalitions are predicted to change across populations with varying female reproductive quality. The results of this model predict that coalitions are more unstable and show a greater variation in size when female reproductive quality is more variable. However, the influence of variation in female quality should be mediated by additional social factors including group size, variance in male competitive ability, sex ratio and reproductive skew. Placing cooperative coalition formation in the context of competition is a strength of this thesis: while coalition formation is often understood within the spectrum of cooperative behaviours (e.g. Díaz-Muñoz, DuVal *et al.* 2014), this behaviour additionally facilitates variation in competitive success. Indeed, by considering coalition formation a competitive strategy, we are able to identify the breadth of influence social factors, such as sex ratio and variance in competitive ability, have across a range of competitive strategies.

6.2 Competition in the Absence of Resources

According to the definition provided in the introduction of this thesis; competition is predicted to arise between individuals when resources are limited. However, Chapters 2 and 4 describe aggressive behaviours in the absence of an obvious contestable resource. Why then, did aggression arise within these studies?

In Chapter 2, we considered aggression among *L. ocellatus* males. Under natural conditions, male *L. ocellatus* compete for mating opportunities by defending territories with empty gastropod shells where one, or multiple, females brood (Bills 1996). When collecting data for Chapter 2, males

were housed both in the absence of females, and in tanks that lacked shells which males could territorially defend. Despite this, we showed in Chapter 2 that aggression still arose among male *L. ocellatus* and varied across stocking densities. Continued aggression in the absence of resources may prime individuals to better access resources once they are available. For example, prior competitive experience could increase the predictability of future contest outcomes, especially when winner and loser effects occur (Landau 1951). This may allow individuals to more strategically engage in favourable contests when resources are present, and the costs and benefits of competition are higher. Alternatively, the absence of resources can provide an opportunity for individuals to 'practice' aggression; improving the chances of competitive success once resources are available (e.g. a more costly version of 'play fighting' which occurs among juveniles in many species; Pellis and Pellis 2017). Future studies in *L. ocellatus* should investigate these suggestions, for example, by comparing the ability of an individual to establish territory in the presence of familiar *vs* unfamiliar opponents once a contestable resource has been provided.

In Chapter 4, we considered temporal patterns in female intrasexual aggression across flocks of red junglefowl with differing age- and sex-compositions. In red junglefowl, sex-specific hierarchies modulate priority of access to contestable resources, including food and mates (Banks, Wood-Gush *et al.* 1979). When collecting data for Chapter 4, females were supplied with food *ad libitum*, which therefore did not constitute a contestable resource. Consistent with this, counts of feeding did not vary across flock types despite observed changes in aggression. Further, while the presence of a male in one flock type may have incited competition among females for mating opportunities (e.g. as occurs in two-spotted gobies (*Gobiusculus flavescens*) under a female biased OSR; Forsgren, Amundsen *et al.* 2004), data collection for Chapter 4 took place outside of the

breeding season. Thus, unlike Chapters 3 and 5, mates were not considered to be a limiting resource promoting competition in Chapter 4.

Intrasexual aggression described within Chapter 4 may instead have arisen through competition for dominance rank itself. Although the anticipated value associated with rank position may have been comparable across flock types, the costs and benefits to females of defending their social rank may have varied, prompting the differences in aggression seen. Examples of aggression to defend, or obtain higher, social ranks ~~can~~ are prevalent in species that form coalitions (e.g. spotted hyenas, *Crocuta crocuta*, and chimpanzees, *Pan troglodytes*; reviewed in Chapter 5; Engh, Siebert *et al.* 2005, Gilby, Brent *et al.* 2013). While hierarchies evolve to reduce costs from enduring aggression among individuals, it may be ineffective to continually dispel and re-establish hierarchies in response to resource abundance (Kaufmann 1983, Tibbetts, Pardo-Sanchez *et al.* 2022). Further, when social rank is heritable (e.g. in many primate species and spotted hyenas, though not red junglefowl), dominant individuals may act to establish hierarchies independent of resource availability (Holekamp and Smale 1991).

Alternative to the above suggestions, populations of *L. ocellatus* and red junglefowl in Chapters 2 and 4 may have lacked the behavioural plasticity to 'correctly' respond to their environment by abstaining from aggression in the presence of no contestable resources (Duckworth 2010). In these Chapters, observations of *L. ocellatus* were conducted in single-sex tanks with no spawning substrate, and observations of red junglefowl took place in pens with an abundance of food. Such conditions are unnatural, and captive individuals may persist in maladaptive competitive behaviours despite no direct benefits of doing so. Beyond these considerations, exploring aggressive behaviours of *L. ocellatus* and red junglefowl under the captive conditions outlined in this thesis remains crucially important. *L. ocellatus* are a popular species within the ornamental

fish trade and aggression among individuals is common despite widespread practices to remove spawning substrates. Meanwhile, red junglefowl are the progenitor species to the domestic chicken (*G. g. domesticus*) and show comparable social organisation and behavioural patterns, such that ecological studies on one species can have useful applications for the other (Masure and Allee 1934, Collias and Collias 1967, Pizzari 2016). In 2023, worldwide annual poultry production is predicted to increase to 140 million metric tons, though resulting egg and meat yields may be reduced when aggression has negative impacts on the health and survival of individuals (OECD and FAO 2023). Understanding the social drivers of competition among domestic chickens under captive (farming) conditions is thus of profound economic relevance. More broadly, competition is a problem in many captive species, from pets to zoo animals, though individual welfare is often improved by being part of a group (Maple and Perdue 2013, Rommers, Reuvekamp *et al.* 2014, Wolfensohn, Shotton *et al.* 2018). Research (as conducted in this thesis) may help to identify the extent to which these harmful behaviours can be managed in captivity and to assess the suitability of different species for this (Koene 2013).

6.3 Future Directions

6.3.1 Incorporating Trade-offs

Strategic investment in competition is expected to maximise individuals' fitness and thus evolve through processes of natural and sexual selection (Darwin 1859, Darwin 1871). However, competitive strategies may trade off with additional factors, including intersexual selection (i.e. mate choice) and longevity, that influence fitness. Consideration of these trade-offs is important for gleaning more precise estimates of the evolutionary significance of strategic investment in competition.

Intersexual Selection

Competition between individuals for access to mating opportunities comprise only one aspect of sexual selection (Darwin 1871). Indeed, mates are not an inert resource and successful reproduction should additionally depend on the direction of intersexual selection, that is, which individuals are preferred by the opposite sex. Examples of intrasexual selection altering the outcome of competition may be seen, for example, in great snipe (*Gallinago media*). In this species, females fight for access to repeated copulations with preferred males, though such males refuse to mate (and even chase away) females that they have already mated with, altering the outcomes of intrasexual competition (Sæther, Fiske *et al.* 2001). Even when one sex has the ability to coerce the other into mating, post-copulatory mechanisms can modulate opportunities for reproductive success. For example, in feral domestic fowl, females bias sperm retention in favour of preferred (dominant) males by ejecting ejaculates of subordinate males following copulations (Pizzari and Birkhead 2000).

In many cases, individuals favoured by mate choice are those that are successful in intrasexual competition (Cox and Le Boeuf 1977, Qvarnström and Forsgren 1998, Pizzari and Birkhead 2000). Preference for more competitive individuals may be beneficial when this confers direct benefits (e.g. access to better territories; Buchanan and Catchpole 1997) or indirect benefits (siring successful offspring of the competitive sex, e.g. Kempenaers, Verheyen *et al.* 1992) (Wong and Candolin 2005). Signals of competitive ability (e.g. badge size; Møller 1990) may be co-opted as cues of mate choice if these are frequently tested in combat and hence are unlikely to falsely advertise quality (Berglund, Bisazza *et al.* 1996). However, highly competitive individuals may not always be preferred by members of the opposite sex. For instance, when parental care is an important predictor of reproductive success, a ‘good parent’ (rather than a competitive partner)

may be preferentially sought by the choosy sex (e.g. as in sand gobies, *Pomatoschistus minutus*; Forsgren 1997). Further, individuals may actively avoid copulation with victors of intra-sexual competition if the latter are particularly aggressive (e.g. Moore and Moore 1999), mate competition and parental care trade off (reviewed within Stiver and Alonzo 2009), or when there is a perceived risk of genetic incompatibility (reviewed within Tregenza and Wedell 2000).

Altogether, the influence of competitive outcomes on reproductive success may be limited when directions of inter- and intrasexual selection become uncoupled. As such, costs and benefits of strategic investment in competition should also depend on the opportunity and direction of mating preferences. In Chapter 5, we used a theoretical model to predict that males should form larger coalitions within certain social environments; such as those with increased variance in female quality. When there is large variation in reproductive quality among females, males may benefit from forming large, competitive coalitions to access higher quality mates if the value of associated reproductive opportunities outweighs the cost of sharing. In barbary macaques (*Macaca sylvanus*), mid- to low-ranking males are most likely to form coalitions to access mating opportunities (Bissonnette, Bischofberger *et al.* 2011). However, females in this species show preference for more competitive individuals, which may reduce the frequency with which coalitions arise. Future work, and especially theoretical models where intersexual interactions may often be ignored, should take care to incorporate the role of mate choice to better understand how competitive strategies arise through sexual selection. Consideration of intersexual interactions will allow the evolutionary importance of intrasexual competition to be better elucidated.

Longevity

The benefits of competitive success under sexual selection may additionally be constrained by natural selection if investment into competition impedes survival. In species with social hierarchies, it is often assumed that subordinate individuals accumulate high levels of physiological stress from frequent attacks by dominant individuals. As such, subordinate individuals may be more likely to incur stress-related pathologies, with negative impacts on longevity (Sapolsky, Alberts *et al.* 1997). However, when dominant individuals are more frequently involved in aggressive interactions, they may experience relatively higher levels of social stress despite an increased likelihood of winning contests (Creel, Dantzer *et al.* 2013). For instance, in the cichlid fish *Neolamprologus pulcher*, dominant individuals are reported to have higher glucocorticoid levels than subordinates (Mileva, Gilmour *et al.* 2011). Further, when dominant individuals monopolise access to mating opportunities, heavier investment into reproduction by these individuals may accelerate senescence through elevated rates of biomolecular damage (Blount, Vitikainen *et al.* 2016). The benefits of competitive success may therefore be limited when this trades off with longevity. Future studies should take care to understand the difference in lifetime reproductive success of individuals with different competitive abilities and/or strategies to better understand the evolutionary significance of this diversity.

Changes to longevity, as a consequence of investment into competition, may additionally vary across social environments. For example, increased population density may generally increase physiological stress (Christian 1950). This may reduce the energetic resources individuals have available to invest into competition if increased somatic maintenance is required to offset the costs of physiological stress (Harshman and Zera 2007). Consequently, variation in competitive ability may be reduced in populations with higher densities, with knock-on effects for the expression of

competitive behaviours (e.g. coalition sizes, as discussed in Chapter 5). Within social environments, interindividual variation in longevity may be affected by the organisation of the social group. In olive baboons (*Papio anubis*), subordinate individuals experienced more physiological stress than dominant individuals when hierarchy stability was high, though the opposite was true when hierarchy stability was low (Sapolsky 1992). Although we showed this not to be the case for red junglefowl in Chapter 3; reduced hierarchy stability may emerge within populations where individuals are similar in their competitive ability across some species (Vaughn and Waters 1981, Dehnen, Papageorgiou *et al.* 2022). Variation in hierarchy stability may therefore place differential constraints on group members' expression of competitive traits, if dominance rank has a varying effect on longevity.

6.3.2 Quantifying costs and benefits of competition

Throughout this thesis, changes in behaviours (including aggression, mating, courtship and coalition formation) were assumed to occur in response to changing costs and benefits of competition. However, studies rarely quantify these costs and benefits alongside measures of behavioural changes. This can impact both our understanding of how competitive success can improve fitness, as well as predictions for when competition should arise. Below, I make some suggestions on how quantifying the costs and benefits of competition could be used to extend the findings of this thesis.

In Chapters 2, 3 and 4, intrasexual aggression among individuals was assumed to incur costs, including physiological stress, energetic expenditure and risk of injury. Future studies should incorporate measures of such costs. For example, cortisol levels have been suggested to reflect variation in physiological stress in fish (Earley, Edwards *et al.* 2006). Future studies in *L. ocellatus*

may compare cortisol levels to test the suggestion that the stress incurred across opponents is lower in higher stocking densities, where we showed aggression became increasingly restricted to larger individuals. Further, future studies investigating the influence of flock composition, sex ratio and environmental complexity on competitive behaviours in red junglefowl may quantify costs of energetic expenditure and injury risk by measuring changes in body weight and feather pecking (which can result in tissue damage; Savory 1995), respectively. Special care should be taken here, however, to identify (e.g. through behavioural observations) which costs are directly associated with competition and which are related to subsequent outcomes (e.g. female weight loss if male harassment leads to avoidance of feeding, or feather loss as a result of preening to relieve stress) (Bhagwat and Craig 1979, Kozak, Rozempolska-Rucińska *et al.* 2019). In Chapter 5, I assumed males incur no costs of coalition formation. However, coalition membership may impose costs when members use aggression to exclude rivals from mating opportunities and expend energy on coordinating attacks (Whitehead and Connor 2005).

Within social environments, quantifying the number of offspring individuals produce across their lifetimes can elucidate the benefits of competition. Further, measures of lifetime reproductive output may be useful in indicating the adaptive significance of competitive strategies in response to trade-offs. In male Columbian ground squirrels (*Urocitellus columbianus*), territoriality is associated with increased reproductive success, but when adopted at a young age this tactic can reduce survival (Balmer, Zinner *et al.* 2019). Low quality individuals may initially be unable to defend territories and should maximise their reproductive output by deferring breeding until the next year. However, some males instead adopt a 'satellite' tactic (living on the periphery of territories established by more dominant males). Although this alternate strategy offers a lower reproductive output (and could be considered a 'lesser' competitive strategy), it may ultimately be

beneficial if mortality between breeding seasons is high (Balmer, Zinner *et al.* 2019). Across social environments (e.g. an increasingly male biased sex ratio), assessing the benefits of shifts in individual behaviours (e.g. increased intrasexual aggression among males) may be challenging in the absence of a control, where no behavioural changes occur. Experimental evolution using short-lived species, such as *Drosophila melanogaster,* where aggression is both plastic and heritable, provides a powerful solution (e.g. Dierick and Greenspan 2006, Chen and Sokolowski 2022). For instance, flies evolving under different conditions (e.g. sex ratios) can be assayed every *n* generations by transplanting them into alternative competitive environments (including control treatments). The lifetime reproductive success of transplanted and evolved (i.e. non-transplanted) flies can then be compared to assess the relative benefits individuals receive from altering their competitive strategies. Studies on this topic have already begun (e.g. Bath, Edmunds *et al.* 2021, Sepil, Perry *et al.* 2022), though further experimental evolution studies are required to explore strategic investment into competition across the broad range of competitive environments outlined in this thesis.

6.4 Concluding Remarks

Throughout this thesis, I have discussed the role of the social environment in influencing strategic investment into competitive strategies, including individuals' propensity for, and distribution of, intrasexual aggression, mating (in response to sperm competition) and coalition formation. Understanding how individuals respond to their social environment is of increasing importance given the pervasion of anthropogenic changes that drive heterogeneity among biotic (and abiotic) factors. Indeed, ecological catastrophes (e.g. oil spills), urbanisation, and eutrophication from modern farming techniques may have a severe influence on affected populations; skewing sex

ratios, limiting variance in competitive ability and reproductive quality and altering how individuals perceive their social environment (e.g. Martínez-Abraín, Velando *et al.* 2006, Liker, Papp *et al.* 2008, Gilby, Olds *et al.* 2020). In addition, reduced natural habitats, and growing concerns over food security beget an urgent need to understand how costly competition can be managed in captive species. Understanding how individuals respond to their social environment thus stands out as a crucial avenue for research in this changing world, and is a topic contributed to by this thesis.

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