A systematic review of methodologies for studying behavioral imprinting

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Abstract

Behavioral imprinting is a learning phenomenon by which animals acquire preferences for stimuli by perceptual exposure during critical periods, without substantial external reinforcement. Since being acknowledged in 1516 by Sir Thomas More in artificially incubated domestic chickens, imprinting has been reported in diverse species, across various sensory modalities, and during different life-history stages. Due to this diversity, imprinting research uses highly varied methodologies, with distinctive differences between the methods employed for different types of imprinting. We systematically review relevant literature, identifying and describing the range of methodologies used to study imprinting across taxa and modalities. After compiling a representative dataset of 192 behavioral imprinting-focused experiments, we categorize studies by imprinting modality, focal species, ontogenetic stage addressed, and methods applied for both exposure and testing. The majority of studies in the sample focus on filial imprinting in precocial birds but non-filial types, such as sexual or home range imprinting in altricial and non-avian species are also present, albeit at far lower proportions. Filial imprinting is studied across different sensory modalities, mostly through applying artificial stimuli, but non-filial imprinting studies mainly use live animals as stimuli, without isolating the relevant sensory modalities. Most studies of filial imprinting measure preference by spatial proximity, following response, or the suppression of a fear response, whereas most studies of sexual imprinting employ the attempt frequency of sexual behaviors. Finally, we analyze the relative frequencies of methodological approaches in each imprinting category, to highlight potential biases due to uneven research effort rather than intrinsic biology. The patterns and biases in imprinting methodologies that we uncover hamper attempts to establish whether different forms of imprinting share mechanistic foundations, including whether imprinting constitutes a biologically meaningful learning category.

Keywords: behavioral methods, heatmaps, imprinting, review

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Introduction

Many types of animal behavior are guided by social experiential processes, including some responses and preferences essential for survival and reproduction that need to be imprinted, meaning that they are learned through perceptual input during specific stages of ontogeny. Although long known to animal breeders, and already described in Sir Thomas More's 1516 novel "Utopia", behavioral imprinting did not feature in scientific literature until 1873, when Douglas Spalding, one of the founders of ethology, described what he believed to be an innate instinct in young domestic chicks (*Gallus gallus domesticus*) to follow the first moving object that they had seen (Gray 1963). It was then studied extensively and popularized by ethologist Konrad Lorenz and his mentor, Oskar Heinroth, through behavioral experiments on hatchling waterfowl. Lorenz (1937) described it as a specific form of learning that is both unreinforced and irreversible, labeling it with the German word "*Prägung*", which can be translated as "imprinting". Such behavioral imprinting (as opposed to genomic imprinting; *sensu* Reik and Walter 2001) is presently defined as a learning process in which an individual's preferences and/or behavioral responses are restricted to a specific perceived releaser stimulus after unrewarded exposure (McCabe 2013). Furthermore, the process may rely on innate predispositions for certain traits of candidate stimuli, and on exposures during short and specific time periods in the organism's ontogeny known as sensitive periods (Hess 1964).

In most natural imprinting systems, the type and amount of movement of the candidate stimuli are highly influential. Wood and Wood (2021) showed that, for young domestic chicks, motion cues support object perception from the earliest stages of development. Additionally, naïve chicks have been shown to exhibit an innate preference towards biologically plausible motion patterns compared to random motion (Vallortigara, Regolin, and Marconato 2005; Miura and Matsushima 2016). Thus, researchers frequently use moving stimuli compatible with established preferences, in order to ensure robust imprinting effects.

A wide range of different learning processes that fit the definition of imprinting, and specially its 'unreinforced' property, have been reported in diverse groups of animal lineages both within and outside of the avian class. Distinct types of imprinting phenomena, such as filial, sexual, and territorial imprinting, are differentiated in the literature by different ecological contexts of behavioral preferences (Gottlieb 1961; Klinghammer and Hess 1964; Scholz et. al. 1976; Burghart & Hess 1966; Arvedlund & Engdahl-Nielson 1996; Sievert et. al 2020). Because of the focal and relatively stable nature of behavioral imprinting, imprinted preferences have drastic effects on a multitude of developmental systems. From prey choice to conspecific recognition, from sexual preferences to migratory pathways, organisms rely on imprinting to enable the reliable and long-lasting acquisition of fitness-relevant learned behaviors (Burghart and Hess 1966; Hansen, Johannessen, and Slagsvold 2009; Schutz 1965; Scholz et al., 1976).

Although different forms of imprinting share similarities, many of these forms are distinct and their study demands different experimental approaches. One important characteristic in which imprinting forms differ is by the amount of generalization associated with the acquired preferences (Immelmann 1975). This level of preference generalization is dependent on the various ecological demands associated with each developmental process. For instance, filially imprinted preferences are logically assumed to involve levels of resolution and detail sufficient to successfully recognize specific individuals as "my parent". In contrast, sexual, host, and diet imprinting allow for a higher level of preference generalization, such that the acquired preferences can be applied to an entire species or other class categories of individuals. As

Bateson (1978) proposed, sexual imprinting may have evolved repeatedly to ensure the recognition of an intermediate degree of similarity between members of a brood and later preference for mating partners. Phenomena such as sexual imprinting may be associated with wide generalization at mate selection time (e.g., species recognition), with narrowing discrimination after socially monogamous pairs are formed (e.g., mate recognition; Campbell and Hauber 2010). These fluctuations may, in many species, vary cyclically, re-occurring in successive reproductive seasons. Indeed, the control of generalization may become one of the most interesting arenas for imprinting research, since it promotes the integration of adaptive reasoning with proximate and mechanistic accounts.

Because imprinting phenomena exhibit diverse behavioral characteristics in development, sensory perception, ontogeny, and adaptive function, researchers employ equally diverse experimental methods. However, methodological differences may lead to a lack of cross-talk between different groups of experimenters who employ distinct tests and trials and may also result in over- or under-generalizing specific observations and patterns of unreinforced learning phenomena within each methodological approach. Thus, when observed properties of imprinting phenomena differ, it can be impossible to discriminate between genuine biological differences and consequences of differences in methodology. The purpose of our systematic review of the literature is to help unravel such potential biases through the explicit identification of the range of behavioral methodologies used in this scientific field, and in the process, identify underrepresented study systems and imprinting processes. While previous critical reviews focused on the properties of imprinting (Klopfer 1964; Immelman 1972; Immelman 1975; Bateson 1966; Bateson 1979, Bolhuis 1991, ten Cate and Vos 1999; McCabe 2013), we specifically address experimental methodologies in order to complement those reviews and help build a broader perspective of the field examining dedicated, adaptive, and unreinforced forms of learning. It is worth noticing that vocal learning, especially song learning in birds, shares properties with behavioral imprinting (ten Cate et. al 1993) and may well be supported by similar neural structures and processes. However, song learning has developed as a vast and independent field, and for this reason we do not include it in the present report.

Methods

Literature search

The sample dataset

To generate a representative data set, we performed a search through Web of Science (WOS), using the default “search in all fields” setting and the following search string: ["avian imprinting" OR "behavioral imprinting" OR "filial imprinting" OR "sexual imprinting" OR "altricial imprinting" OR "precocial imprinting" OR "visual imprinting" OR "tactile imprinting" OR "auditory imprinting" OR "olfactory imprinting" OR "classic imprinting" OR "natal imprinting" OR "semi-precocial imprinting" OR "semi-altricial imprinting"]. This search was performed on April 30th, 2023. To create a dataset that was repeatable in future years we limited our search criteria to exclude all papers published partly through 2023. This search resulted in a dataset containing 496 unique publications. It is important to note that using these search parameters, we are leaving earlier works that have yet to be digitized into a searchable format out of our collection, as well as papers that conceptually should be included but did not use our specific set of wordings in the title or content.

Data Evaluation

For reasons of manageability, studies that investigated behavioral imprinting strictly through non-behavioral (e.g., physiological, neurobiological) means were removed from our dataset. For instance, Yamaguchi et. al (2011) investigated the neural mechanisms of imprinting by examining gene expression in the brains of juvenile domestic chickens pre- and post-imprinting but did not behaviorally test for imprinting directly and was, thus, removed from our dataset. In contrast, Lowndes, Davies, and Johnson (1994) investigated the neural mechanisms of imprinting in chicks by administering lesions to different areas of the brain and then behaviorally testing for any differences in the chicks' imprinting capabilities. Since this latter paper used behavioral testing methods, it was included in our dataset. Altogether 202 papers were removed for using strictly physiological methods to investigate imprinting, 135 of which strictly investigated neurobiological aspects of such learning. A further 81 papers were removed for being reviews themselves, conceptual discussions, or quantitative evolutionary models. Another 21 papers were removed for either not relating to imprinting, not being peer-reviewed, or for being redacted. And lastly, 16 papers found in our WOS search did not have accessible digital English copies and were therefore not included in our dataset. In total, only 176 out of 496 (35%) papers found within our WOS search were accessible peer-reviewed articles that used behavioral methods to investigate imprinting.

We categorized each paper in our 176-article dataset with regards to the kind of imprinting phenomenon studied, taxonomic group included, the behavioral response metrics involved, the sensory modality examined, the age of the subjects used during training and testing, and, for the type avian species tested regarding whether they had altricial or precocial young. For papers that presented experiments with multiple aspects in any of these categorical attributes, we considered each unique combination of tests as a separate experiment. For instance, Grier, Counter, and Shearer's (1967) paper on filial imprinting in the domestic chicken tested for prenatal as well as juvenile auditory imprinting and used different testing methodologies for each. This paper was considered 2 separate experiments for the purposes of this review. In total, 16 studies needed to be divided during our review, bringing the total number of unique experiments to n=192.

The parameters for our six categorizations are defined as follows:

1. We found six distinct groups of imprinting phenomena studied: filial imprinting, sexual imprinting, host imprinting, diet choice imprinting, territorial imprinting, and predator imprinting. Categories for filial and sexual imprinting were defined by the classic descriptions of Lorenz (1937), Schutz (1965), Bateson (1966), and Immelmann (1972). As their terms imply, host, meal choice, predator, and territorial imprinting categories were defined as phenomena which involve exposure to a specific stimulus during a distinct sensitive period that respectively influenced an individual's preference towards a certain host species, preference towards a species of prey, avoidance of a specific predator, and the ability to return to a given site of residence if displaced.
2. Taxonomic groupings were first categorized by class and all avian studies were further categorized by order.
3. The behaviors measured when testing for imprinting were categorized as either the follow response, spatial association, sexual behavior, meal choice, fear response, or other.
4. Our categorization of sensory modality determined whether the study isolated any specific sensory modality during both the training and testing of the individual and what that modality was (visual, auditory, haptic, or olfactory).

5. The age of the test subject was classified as: prenatal, juvenile (an individual dependent on parents and sexually immature), independent (an ecologically competent, “fledged” individual that is capable of feeding itself yet still sexually immature), and adult (a sexually mature individual).
6. Last, all avian species were categorized as either altricial, precocial, or semi-precocial using Starck and Ricklefs’ definitions of these ontogenetic trajectories (1998). Due to the avian-specific nature of Starck and Ricklefs’ definitions, we excluded all non-avian studies from this ontogenetic categorization.

Results

Lorenz (e.g., 1937) launched the modern scientific study of imprinting through his study on the filial attachment phenomena in precocial waterfowl. The fundamentals of his experiments and its design appear to still be the most prevalent, since the number of precocial studies within our dataset chronologically grew earlier and remains more numerous than that of altricial and non-avian studies (Figure 1). The number of studies focusing on sexual imprinting shows a sharp increase after the year 1990 (data not shown), but still, the most numerous category of studies in our sample focused on filial imprinting in precocial birds (71/192 | 37%; Figure 2). Avian taxa are also the most frequently studied lineage (132/192 | 69%), with precocial fowl (Galliformes) making up roughly half of that category (68/132 | 52%; Figure 3). Critically, however, our representation of avian orders is often skewed due to specific, frequently studied, model organisms which could potentially limit the generalization of the results upon the broader taxonomic groups. For instance, the majority of studies which our review categorized under “Galliformes” focused their investigation on the domestic chicken (49/68 | 72%) and half of our review's "Passeriformes" studies focused their investigation on the zebra finch (*Taeniopygia guttata*; 20/39 | 51%). Studies on non-avian taxa were grouped into one single category within our results but included the classes of Actinopterygii, Amphibia, Arachnida, Arthropoda, Chromadorea, Gastropoda, Mammalia, and Reptilia (Figure 4).

Training Methods

Almost all imprinting studies covered here studied captive-raised test subjects in a controlled laboratory environment (166/192 | 86%). The few studies that did not use captive raised animals employed creative and unique techniques in order to study imprinting outside of a controlled setting. For example, Hansen, Johannessen, and Slagsvold (2009) tested for sexual imprinting in wild great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) by cross-fostering nestlings and comparing conspecific versus heterospecific mating associations and intrasexual competition after the test subjects reached sexual maturity.

Studies varied more as to whether they used living organisms or artificial objects as stimuli; this variability depended largely on the type of imprinting studied. Only 18% of studies that studied filial imprinting (17/93) used live animals as stimuli. Conversely, 88% of sexual imprinting studies (72/82) used live stimuli. This recurrent use of artificial stimuli allowed filial imprinting studies to better isolate relevant sensory modalities relative to the sexual imprinting experiments (Figure 5).

Although the exact timing of an individual's sensitive period varies between species and imprinting phenomena, the majority of reviewed imprinting studies (164/192 | 85%) imprinted the subjects when they were juveniles. Even though subjects were most commonly trained as juveniles, sensitive periods were found across all age categories in our sampled studies except for adult (Figure 6). For instance, prenatal sensitive periods were found in the domestic chicken (Grier, Counter, and Shearer 1967) and the bank vole (*Myodes glareolus*) (Sievert et. al 2020) respectively. In turn, 26 studies found sensitive periods during the post-independence/pre-sexual maturity age-range.

Testing methods

The traits and responses measured when testing varied with the type of imprinting being tested. Since each form of imprinting concerns different elements of the organisms' behavioral repertoire, it follows that the approaches to studying these behaviors should be equally variable (Figure 7). Unsurprisingly, the behavioral responses being measured affected the age at which imprinted preferences were tested. Accordingly, filial imprinting was tested for in juveniles in 87% of the studies (81/93) whereas sexual imprinting was, by necessity, exclusively (100%) tested for in sexually mature adults (82/82).

Filial imprinting

When testing for filial imprinting, the two most common dependent variables were the follow response and spatial proximity. These two measures comprised 84% (78/93) of the filial imprinting studies, while the remaining 16% (15/93) used either a fear response, a begging response, an imitation response, or weight gain as indirect measurements of imprinting.

In filial imprinting studies that used spatial proximity, imprinting was tested through behavioral choices between stationary stimuli. All such choice trials used at least one stimulus which was a pre-exposed and another which was novel. There is one exception to this approach, however, in Matinho and Kacelnik's 2016 study on mallard ducklings (*Anas platyrhynchos* *domesticus*). These authors tested the capacity for ducklings to filially imprint on the concepts of same vs. different by exclusively using pairs of novel stimuli during the testing phase. We found 7 spatial proximity tests that used a live animal as the stationary stimulus, in these cases the stimulus individual was confined and isolated (Mattson and Evans 1974; Gerlach et. al 2008; Gerlach et. al 2019; ten Cate 1989; Carter and Marr 1970; and Pallante, Rucco, and Versace 2021). Even within the spatial proximity test category, measurements used to gauge imprinted preference strength varied between the individual's first choice, the number of approaches an individual made to a stimulus, the latency to approach, or the length of time an individual spent near a stimulus (Figure 8a).

In contrast to the spatial proximity tests consistently employing a multiple-choice test between stationary stimuli, studies which used the follow response to measure filial imprinting varied evenly between using the multiple-choice stationary stimuli design (15/29 | 52%) and the single-choice locomotive stimulus design made popular by Lorenz (e.g., 1937). These studies gauged imprinting through either the distance covered while following, the amount of time spent following, or a dichotomous separation of "followed" or "did not follow" (Figure 8b).

Non-filial imprinting

Within our sampled studies, sexual imprinting was most often measured through the frequency of sexual behaviors (37/82 | 45%, Figure 8c) with spatial proximity being the second most common metric (28/82 | 34%). The remaining 17 studies investigated sexual imprinting in humans by administering questionnaires regarding sexual preference to human adults and comparing their responses to the physical attributes of the individual's parents.

Studies that looked at territorial imprinting, host imprinting, predator imprinting, or meal choice imprinting used unique measures to test for imprinting. Territorial imprinting (10/192 | 5%) was tested for in a variety of salmon species (*Oncorhynchus sp.*), Manx shearwater (*Puffinus puffinus*), Blanding's turtle (*Emydoidea blandingii*), loggerhead sea turtle (*Caretta caretta*), and cardinalfish (*Apogon doederleini*) by either judging their propensity to migrate back to an imprinted natal location in the wild or by using spatial proximity within a lab setting. Fig wasps (*Ceratosolen fusciceps*) and bank voles were tested for host imprinting (1/192 | 0.5%) and predator imprinting (1/192 | 0.5%), respectively, and both studies used spatial proximity to an olfactory cue as a metric for imprinting. And last, a diverse group of taxa were tested for meal choice imprinting (5/192 | 3%) through first-choice trials using live prey or through timed spatial proximity tests using olfactory cues.

Discussion

The aim of this review is to identify and describe key similarities and differences in the methodological approaches to studying different imprinting phenomena across a growingly large variety of taxa. We found that the most commonly studied form of imprinting was filial imprinting by precocial birds and these studies made up a larger proportion of our dataset than all the non-avian studies combined (Figure 2). Within this large and multifaceted collection of avian filial precocial studies, the methodologies used for both training and testing imprinting remained relatively consistent. However, the most commonly used methodologies, such as using the follow response as a measurement of imprinting, were not directly transferable to the several altricial studies we observed, since by definition the altricial juvenile subjects are unable to locomote until much later (Figure 7). Altricial bird species have been definitively shown to undergo filial imprinting since the late 1980s (Junco 1988, 1993a, 1993b), yet the methodological difficulties with investigating altricial filial imprinting may contribute towards the dwarfing underrepresentation of altricial filial studies in the literature relative to precocial. It may be possible to experimentally imprint altricial birds during their pre-locomotive phase and test their locomotive responses later in development, however we found no studies which did this.

Our literature search parameters were necessarily imperfect in the sense that they did not find all imprinting articles previously known to us in our authors' team. This is evident, for instance, in the outcome that our literature search did not find any articles related to the concept of parental imprinting. Parental imprinting is distinct from filial imprinting in that in the former the parent restricts parental care towards the young they were exposed to during a specific sensitive period, as found, for instance, in domestic goats (*Capra hircus*) by Hersher, Moore, and Richmond (1958). This paper presents an example of a sensitive period existing beyond sexual maturation, something our dataset did not include. Although not returned by our systematic bibliographic search, this article does fulfil our intended target space because it is available within the WOS database. Additionally, our review only included one instance of host imprinting within a study on fig wasps; however, there is published evidence for host imprinting in the common cuckoo (*Cuculus canorus*; Brooke & Davies 2010) as well as in the clown fish (*Amphiprion ocellaris;* Arvedlund & Nielsen 1996). Therefore, it is possible that other similarly relevant papers within the WOS database were also not drawn into our dataset. We are conscious that such biases are likely to exist in our and other digital bibliographic searches, but they still have the virtue of being reproducible, and likely to be more unbiased and representative of the field than conventional sampling of the literature through personal knowledge or manual searching.

Our review categorized the ages in which subjects were both trained and tested for imprinting (Figure 6). Age categories were originally based on broad avian developmental stages: prenatal, juvenile, fledgling, and adult. Complications arose however once we began applying this categorization across such a wide range of taxa. In order to be more inclusive towards non-avian taxa, categories were redefined as: prenatal, sexually immature and dependent on parents (“juvenile”), independent but sexually immature (“independent”), and sexually mature (“adult”). This new categorization was effective in grouping the different variations in research methodologies, but it nevertheless still introduced inconsistencies. For instance, Schausberger (2005) described an imprinting-like phenomenon of unconditioned learning in predatory mites (*Phytoseiulus persimilis*) with a sensitive period that is ecologically similar to filial imprinting in birds in that it strongly influences the individual’s ability to recognize and appropriately interact with conspecifics. Predatory mites show no parental care and in turn all juvenile mites hatch as what this review would categorize as independent, but sexually immature individuals. Papers similar to this, categorized as an “independent-stage sensitive period”, appear akin to territorial imprinting in many salmon species (*Oncorhynchus sp.*) where imprinting occurs much later in life. However, in contrast, the predatory mite’s imprinting process is more ecologically similar in timing to juvenile-staged filial imprinting in birds than it is to independent-staged territorial imprinting in salmon. It emerges that to compare and contrast imprinting processes and sensitive periods across an increasingly large range of species, a new, more inclusive age categorization system is necessary.

Overall, the studies within this review share one focal similarity: they investigate the acquisition of biologically important preferences and behaviors through unreinforced exposure to a given stimulus configuration during a specific sensitive period. Despite these fundamental similarities, methodologies used when training for, testing for, and classifying imprinting phenomena vary drastically with imprinting type, taxa, and age category. Because of this, there is often ambiguity and gray areas when defining the limits of the biological concept of imprinting. For example, imprinted behaviors and preferences must be acquired before they become biologically relevant (Immelmann 1975). This may apply for most filial and sexual imprinting phenomena; however, it conflicts with what we observed in parental, predator, and diet imprinting studies since these preferences are acquired during the life stage in which they are needed and deployed. As such, the requirement for an imprinted preference to be learned before becoming biologically relevant has been left out of modern literature. This fluidity in the research community's defining parameters can also be seen in the case of parental imprinting, where, instead of a singular sensitive period dependent on an individual's ontogenetic development, there are recursive sensitive periods dependent on reproductive state. While each individual can show filial imprinting once in its lifespan, parental imprinting must occur multiple times in iteroparous species with parental care, and hence sensitive periods for parental imprinting must wax and wane through adult life. Similar considerations apply to seasonal birdsong and host nest book keeping in reproductive parasites, and in such cases biological considerations have served to guide and stimulate neuroscientific research (Clayton et al 1997, Balthazart and Ball 2016). The presence of a sensitive period during a chronologically specific phase of ontogeny is currently used as a defining characteristic of imprinting. This sets imprinting apart from most other forms of learning (Bateson 1979, Tzschentke and Plagemann

2006, Bischof 2007). However, the recurrent nature of sensitive periods in non-filial examples calls for further research. Imprinting-like phenomena in which the emphasis is on a prior, biologically adaptive, predisposition to learn ‘something’ in the absence of obvious reinforcement may be less of a distinct process than it is frequently thought. Sensitive periods for susceptibility to non-reinforcement learning may come to be viewed less as a qualifying factor of imprinting than as expressions of the modulation of all learning by biologically adaptive predispositions (see, for instance, Versace et al 2018).

Within our sample, filial imprinting was the most thoroughly investigated, not only in terms of sheer quantity, but also in the variety of sensory modalities isolated (Figure 5). This deeper understanding of the role of various sensory modalities can be attributed to the fact that a majority of filial imprinting studies use artificial stimuli while most non-filial imprinting studies use live animals as both imprinting stimuli and targets. This use of artificial stimuli also helps to explore less intuitive properties of the content of imprinting. For instance, Monteiro, Hart, and Kacelnik (2021) were able to imprint domestic ducklings onto specific time-structured acoustic stimuli, while in a similar experiment, Martinho and Kacelnik (2016) showed that ducklings were able to imprint on the concept of either “same” or “different” while being exposed to various moving three-dimensional shapes. This shows that birds can filially imprint on abstract, relational properties of their sensory input, rather than simply representing auditory or visual cues, and helps to refine the notion of what constitutes an “imprintable” target. However, artificial stimuli also have significant limitations. Studies of bird song acquisition have found very complex interactions when model song playbacks were accompanied by the visual presence of living adults and artificial stimuli such as stroboscopic flash lights (see Hultsch et al 1999, Hultsch and Todt 2004, Peters et al 2022). This dependence of learning on the social context in which exposure occurs is likely to be significant in the case of imprinting, but it seems to have been mostly neglected so far.

Filial imprinting may be expected to require sufficient specificity to allow subjects to identify individual parents, while phenomena such as host or sexual imprinting may be adapted to identify categories of individuals or even just target species. For this reason, the use of live models for both exposure and testing are also likely to be required. Surprisingly, there is a relatively low number of filial imprinting studies using live animals as stimuli. In contrast, sexual imprinting studies show a proportionally large use of live animals as stimuli compared to those that use artificial stimuli. Since sexual imprinting processes may be expected to show greater generalization, artificial stimuli may help to identify the specific cues individuals use to construct their relatively broad parameters that separate a conspecific from unsuitable alternatives.

In summary, the imprinting literature from the past six decades shows considerable variability in the methods for training, testing, classifying and defining imprinting. This review sheds light on the challenges in defining the term "imprinting" and comparing it across a diverse range of taxa. These difficulties may be mitigated by greater crossing over of both concepts and methods across sub-fields, for instance by greater use of artificial stimuli to study the properties of sexual imprinting, and reciprocally greater use of live stimuli to examine the role of social context in filial imprinting. A systematic comparison of the degree of generalization displayed by various forms of imprinting may also serve to relate the study of proximate aspect of imprinting to theorizing about their adaptive parameters. Determining whether imprinting is a shared phenomenon across diverse taxa and ecological contexts is crucial to deepening our understanding of both the function and the mechanisms of this process. Our behavioral review emphasizes the diversity in classifying and defining imprinting; however, using our methods-focused data base, we are unable to make a definitive claim as to whether the various forms and occurrences of imprinting share genuine biological similarities.

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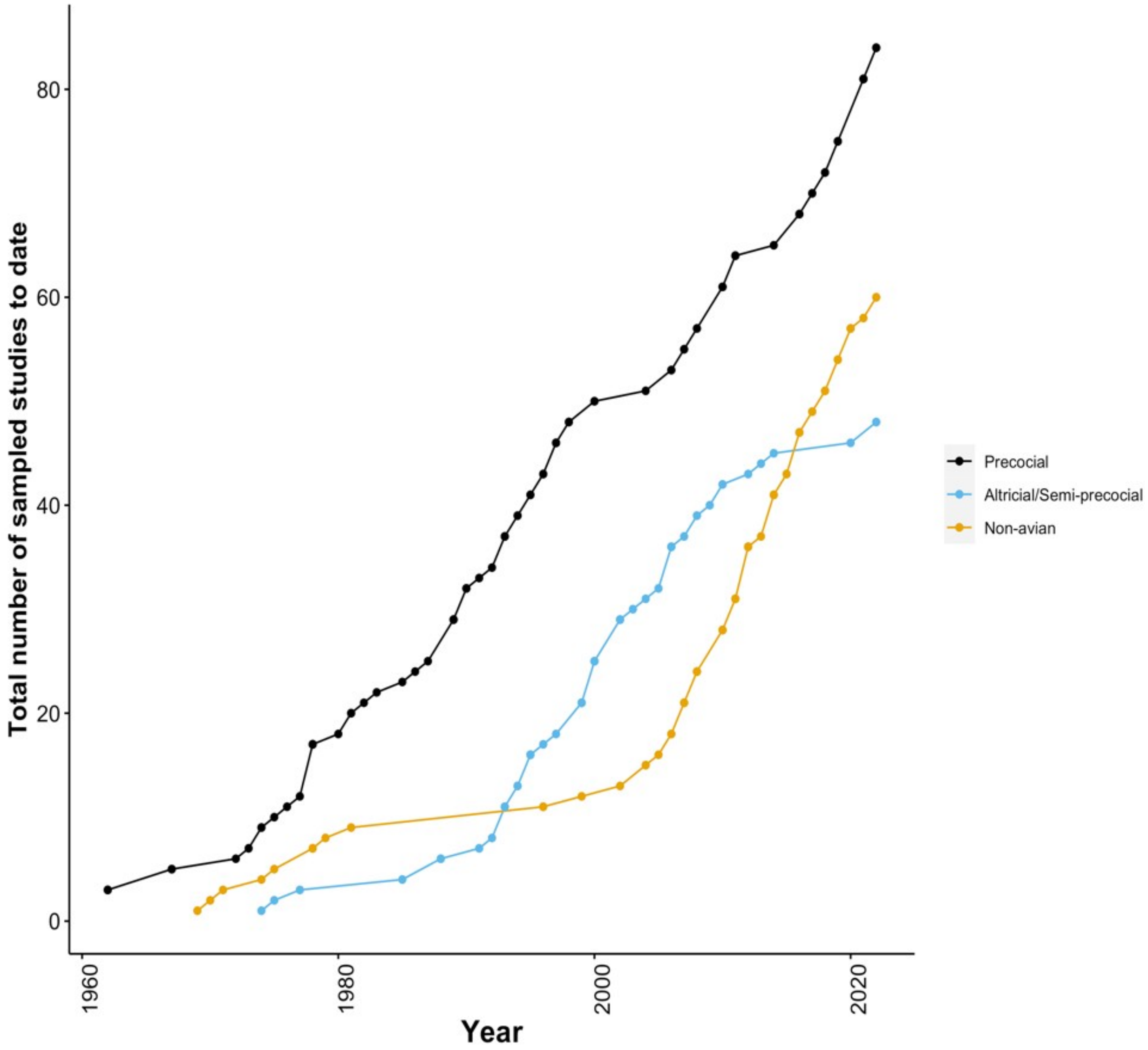

Figure 1: A chronological cumulative growth in total count of sampled studies between three developmental categories: Precocial (black), Altricial and Semi-Precocial (orange), and Non-Avian (blue).

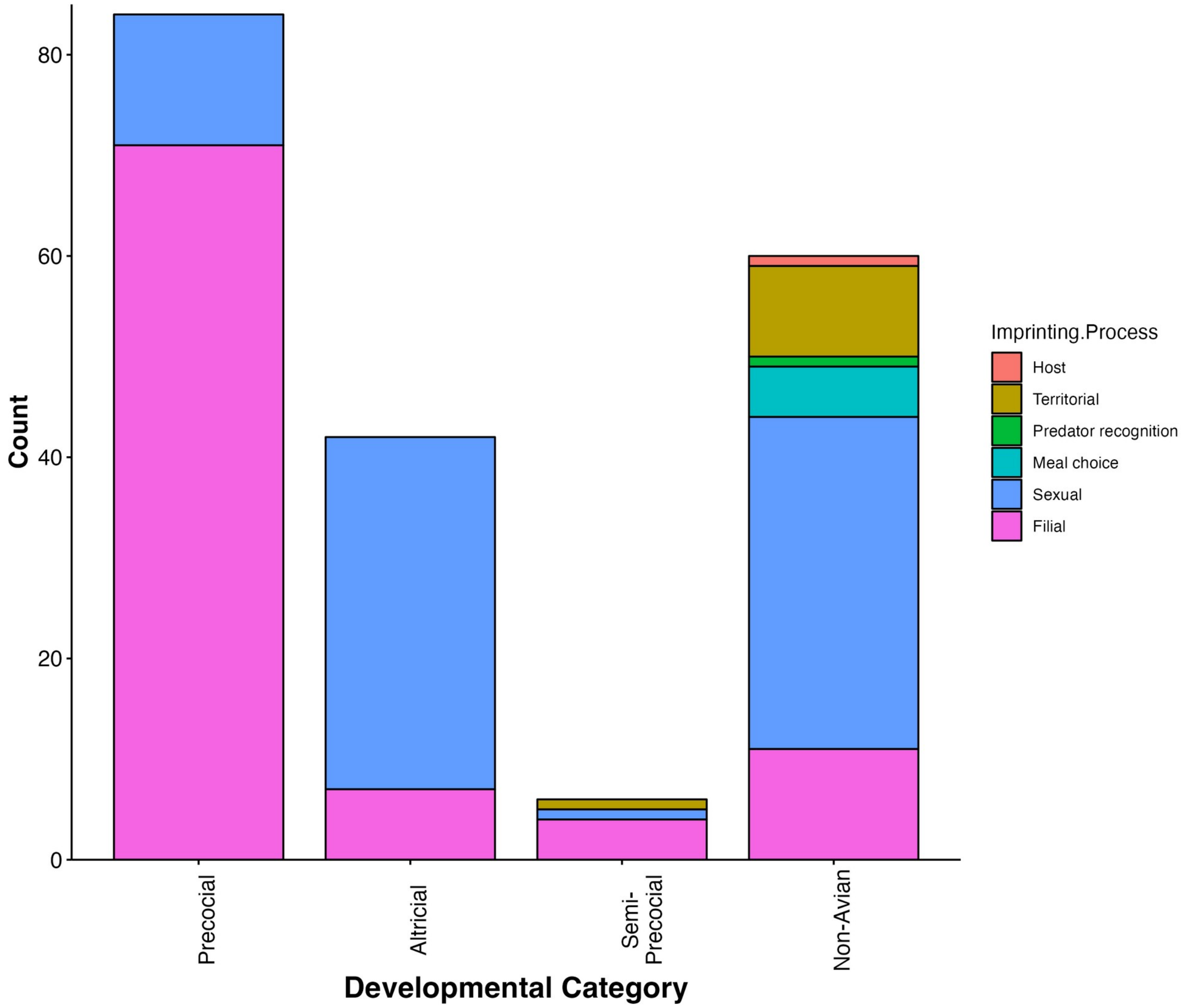

Figure 2: Number of studies within different avian developmental categories that focus on various imprinting processes compared to that of non-avian studies. Avian developmental categories were defined using the parameters outlined by Starck and Ricklefs (1998).

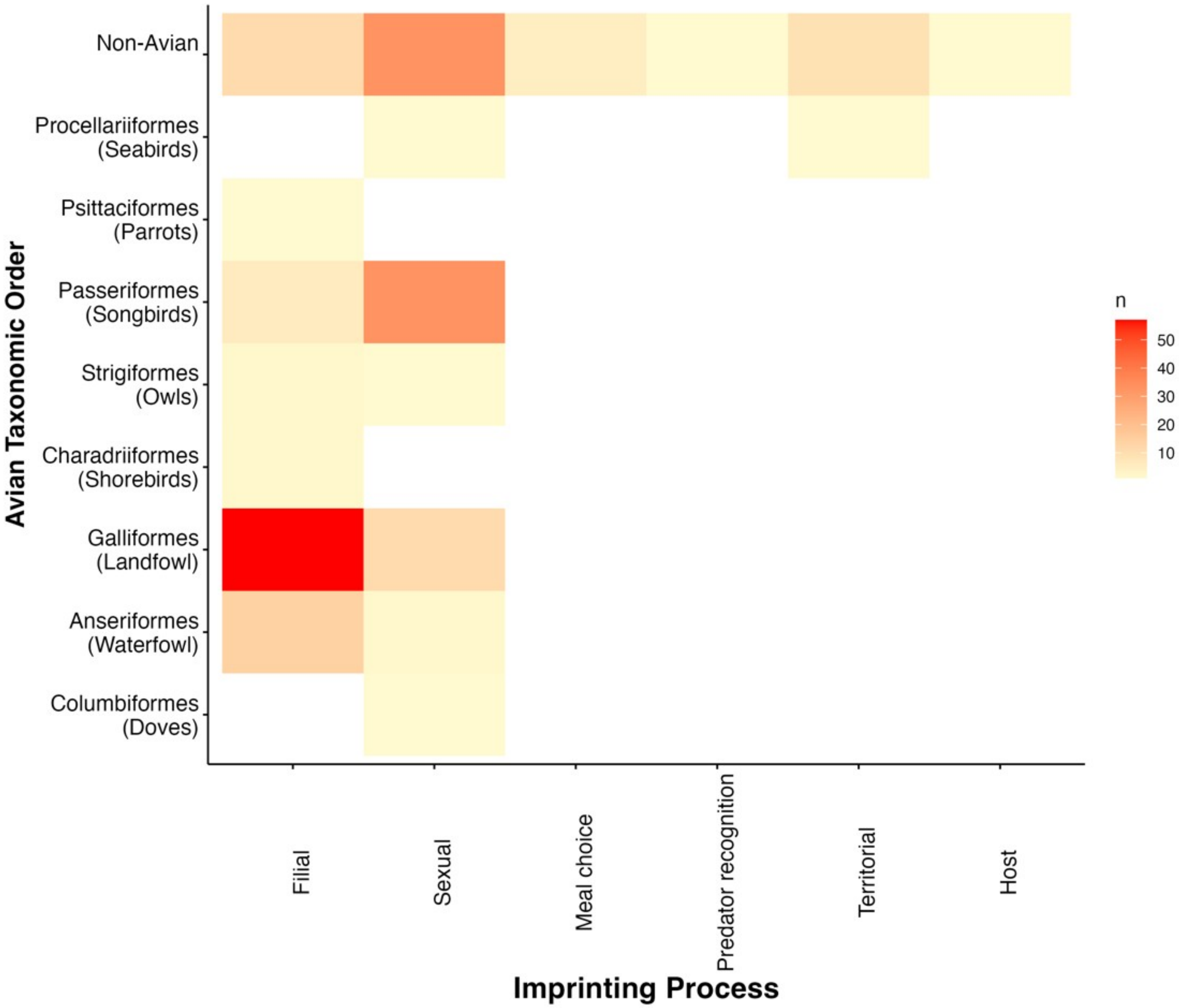

Figure 3: A heat map depicting the quantity of studies classified under both the imprinting process studied and the avian taxonomic order used as a study species.

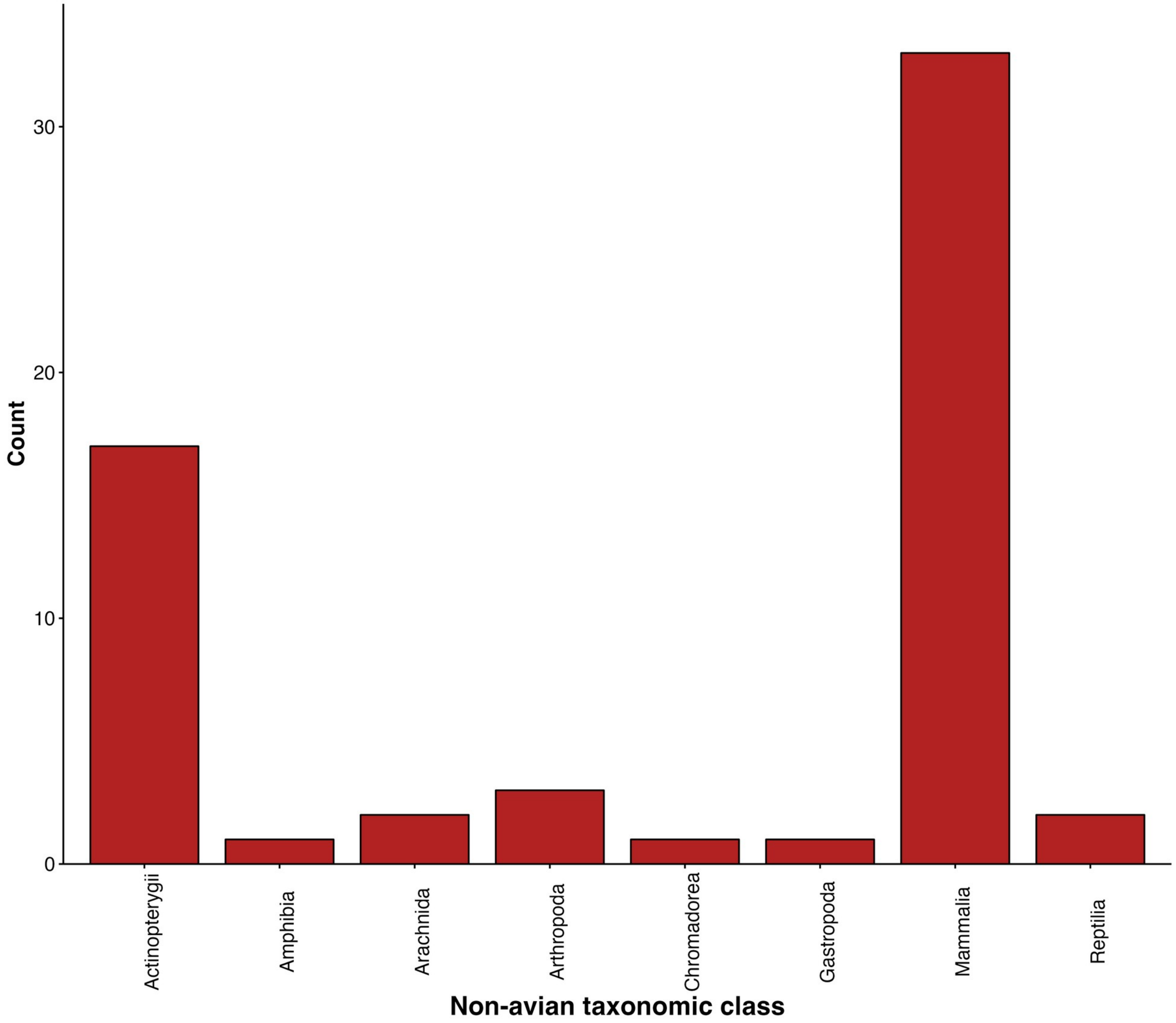

Figure 4: Number of studies within our dataset which used various non-avian taxonomic classes as a study system.

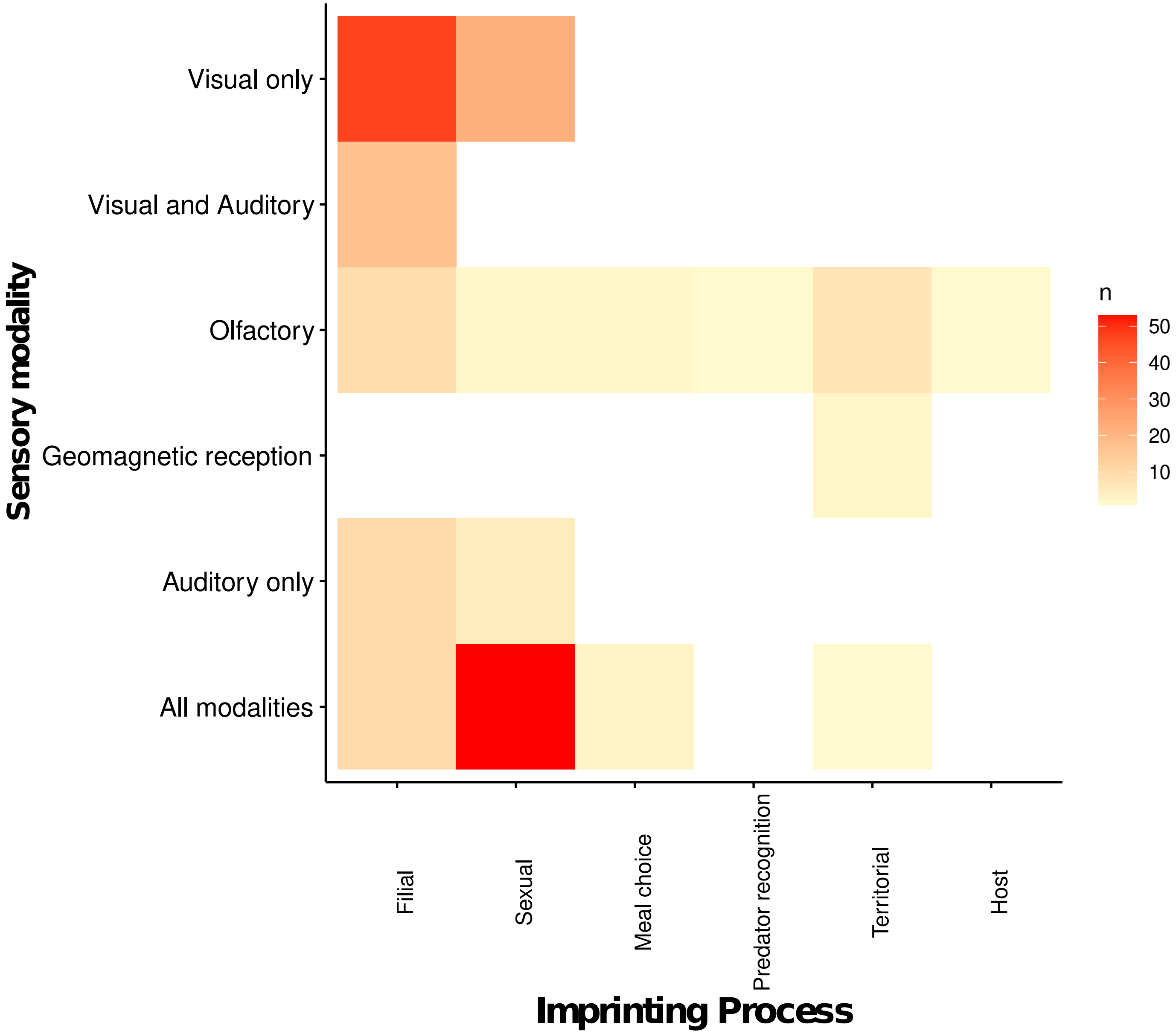

Figure 5: A heat map depicting the quantity of studies classified under both the imprinting process studied and any sensory modalities that were isolated during both the training and testing phases of the study.

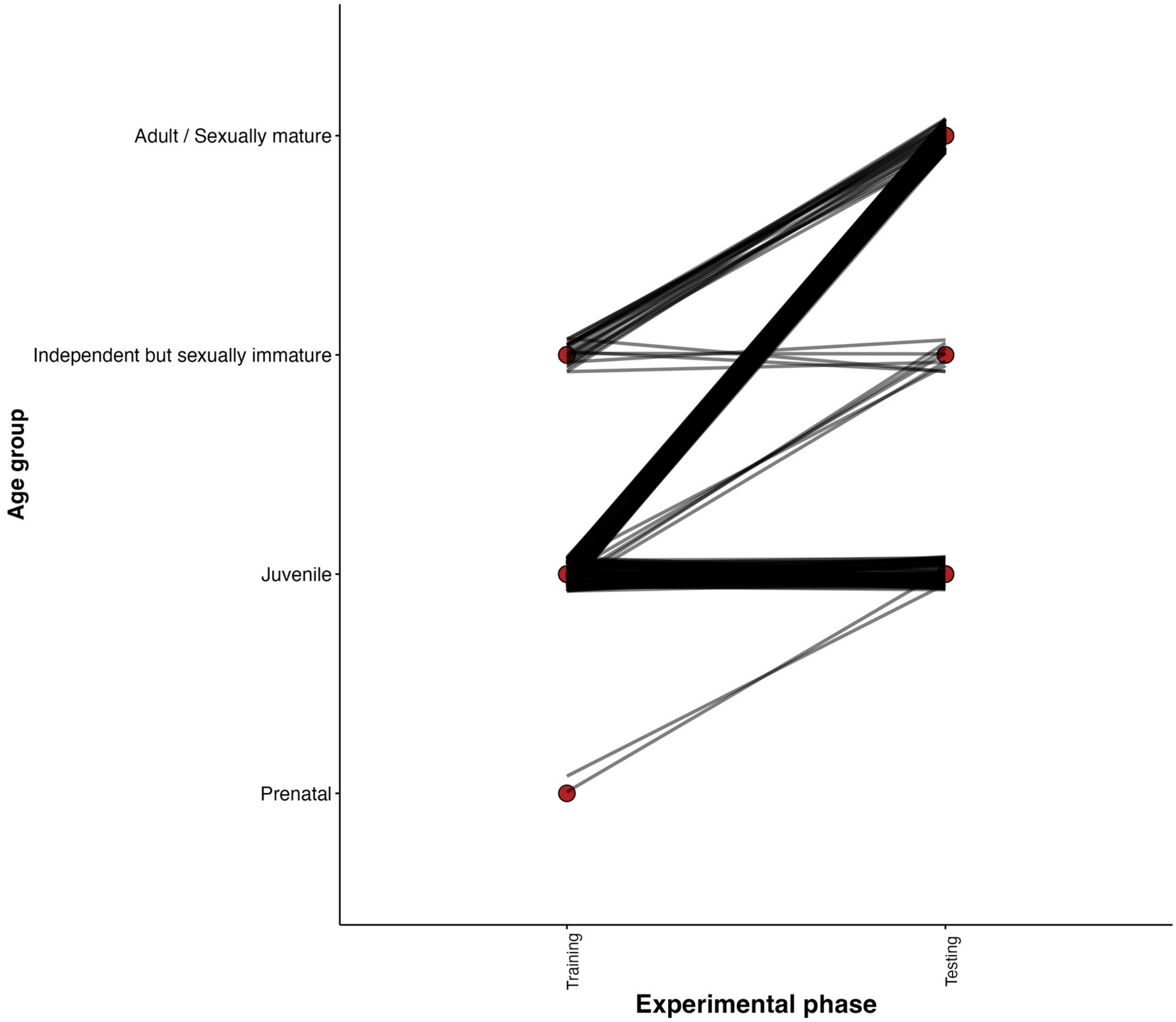

Figure 6: This chart depicts the age category of the test subjects during both the training session (the session in which the test subject is first exposed to the imprinting releaser stimulus) and the testing session (the session in which the test subject's preference towards the imprinted stimulus is measured). The intensity of change between these categories within a single study is depicted by slope and placement of the respective black line.

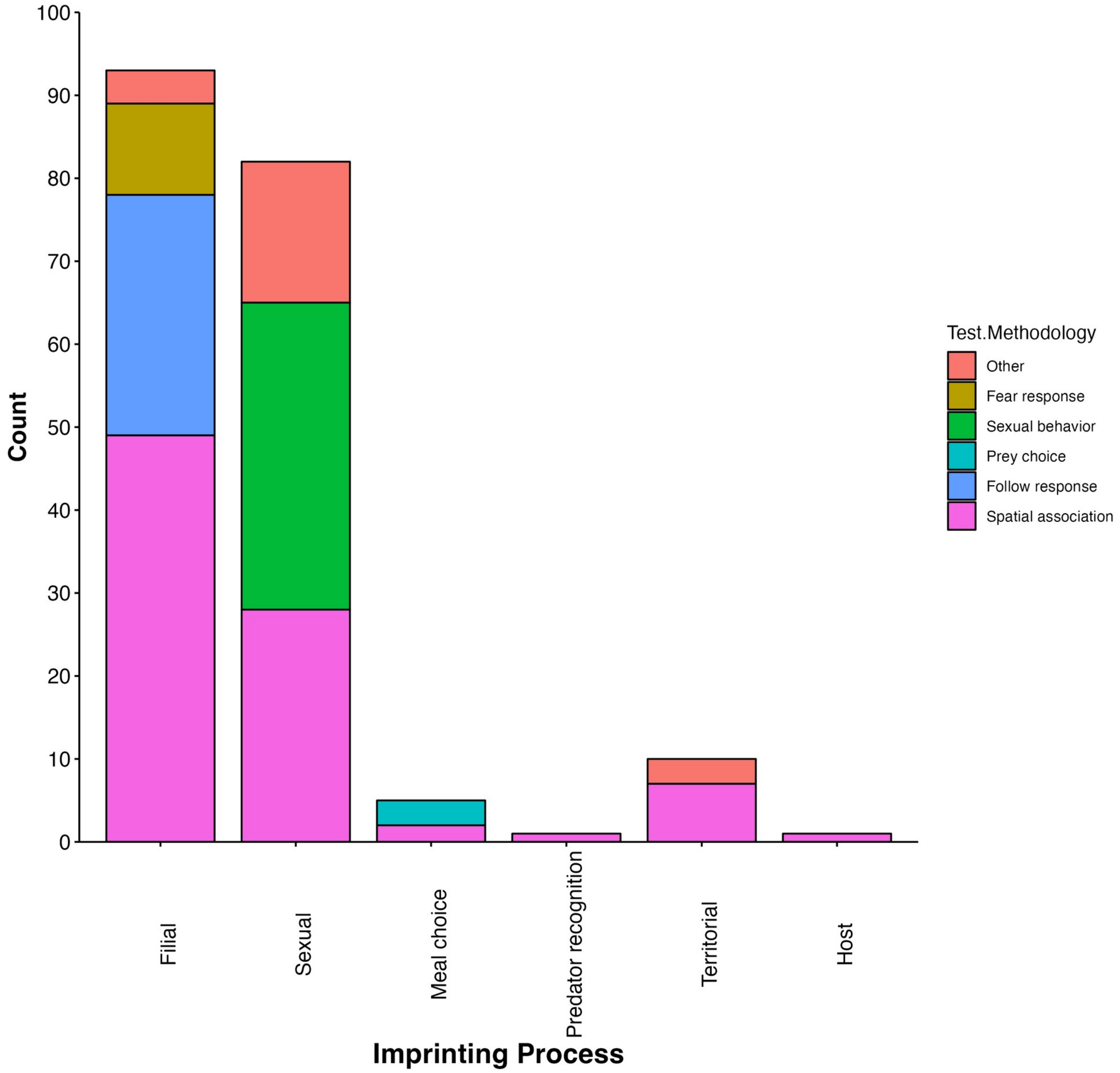

Figure 7: The quantity of studies that focus on the various imprinting processes and methodologies used when testing for preferences toward the imprinted stimulus.

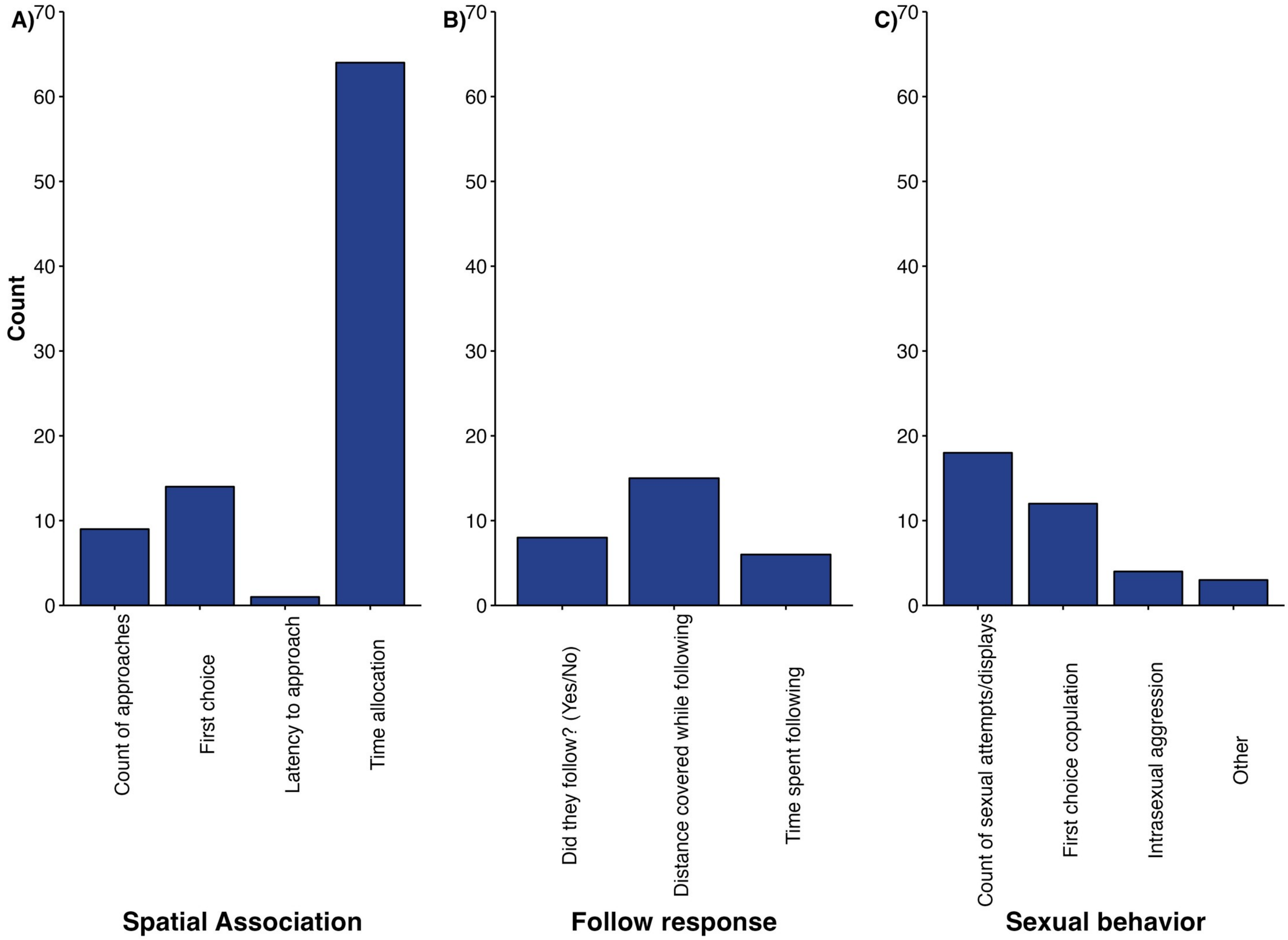

Figure 8: This graph takes a more in depth look within our three most prevalent categories for testing methodologies used while measuring imprinted preference. A) Studies characterized as using spatial association to measure preference are further categorized into the four measurement subtypes: count of approaches, the individual's first choice, latency to approach, and length of time spent near the stimulus. B) Studies characterized as using the follow response to measure preference are further categorized into the three measurement subtypes: the distance covered while following, followed (Yes/No), and length of time spent following. C) Studies characterized as using sexual behavior to measure preference are further categorized into the four measurement subtypes: count of sexual attempts or displays, the individual's first choice for copulation, the level of intrasexual aggression towards perceived conspecifics, and a fourth subcategory of "other" which included mate choice in the wild as well as whether or not a target female investigated a nest.