



AMERICAN
PSYCHOLOGICAL
ASSOCIATION

Volume 133
Number 2

May 2019

Published quarterly

ISSN 0735-7036

Journal of Comparative Psychology

Editor
Dorothy M. Fragaszy

Associate Editor
Todd M. Freeberg

Journal of Comparative Psychology®

www.apa.org/pubs/journals/com

May 2019

Volume 133
Number 2

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Association

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FEATURED ARTICLE ESSAY

From Simple Rules of Individual Proximity, Complex and Coordinated Collective Movement

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Nature may be red in tooth and claw, but it also exhibits innumerable patterns of beauty that elicit wonder. Some patterns are mesmerizing, such as the flight of enormous flocks of starlings and blackbird species at certain times of year (Byrd, 2018) or the swimming of large schools of fish (Handegard et al., 2012). Such movement in flocks and schools often reveals patterns of undulation that seem as though they must have been produced by a master planner, or at least have been activated by a leader. Study of the movement of such flocks and schools suggests, however, that these coordinated patterns often stem from simple rules governing interindividual proximities in space and time (Sumpter, 2010). Indeed, relatively straightforward processes of natural selection can drive such individual-level behavioral decisions, leading to group-level cohesive movement (Ioannou, Guttal, & Couzin, 2012). Greater understanding of these rules and decisions can potentially lead us to the behavioral mechanisms underlying complex group-level behavior.

The empirical study of coordinated collective motion (CCM) has often been built upon the theoretical foundation of mathematical models and computer simulation of behavior (Sumpter, 2010; Vicsek & Zafeiris, 2012). A key theoretical approach to CCM includes the use of agent-based models in which the behavior of individual units is specified into a small number of fairly simple behavior rules (Miller & Page, 2007). Computational models are then constructed around numbers of such individual units interacting with one another, and computer simulations of group-level behavior can be run for various unit population sizes (or other parameter manipulations).

One key assumption of CCM models is that individuals' movement behavior is influenced by rules of proximity—a balance of attraction and repulsion tendencies depending on how close an immediate neighbor is. When individuals are moving in groups, these rules therefore have a bearing on the alignment of individuals in space and time, and so also on the orientation and speed of movement of individuals. As Quera et al. (this issue) point out, however, we have relatively little empirical evidence to support these key assumptions about orientation and speed of movement.

These authors undertook a study in two species of fish, varying group sizes, to assess the validity of these assumptions.

The authors investigated rules of local movement interaction in zebrafish (*Danio rerio*) and black neon tetra (*Hyphessobrycon herbertaxelrodi*; Figure 1). For each species, there were groups of two, three, four, and eight fish, all housed in separate but identical aquaria. Groups were transferred to an experimental tank where their swimming behavior was video recorded for 5 min each, with each group video recorded for 10 days. Samples of frames from each video recording were then analyzed to obtain several measures of individual and interindividual orientation and proximity. Cross-frame comparisons allowed measures of individual turning angles and acceleration.

Quera et al. (this issue) found that smaller groups were generally more cohesive than larger groups. This means that the average interindividual distances across group members were smaller for the smaller groups, despite the higher densities in the larger groups. The authors detected an interesting two-way interaction between group size and species for polarization—the extent to which two fish are oriented in the same direction. Black neon tetra were more polarized (more likely for individuals to be aligned with one another) than zebrafish. Whereas polarization decreased with group size in zebrafish, there was little change in polarization with variation in group size in black neon tetra. Furthermore, in zebrafish but not black neon tetra, individuals were generally located in front of or behind neighbors. In black neon tetra but not zebrafish, short distances between neighbors seem to lead to a repulsion influence for the two individuals, whereas long distances between neighbors seem to generate an attraction influence.

A general set of rules that emerges from this work is that it is most important to avoid collision, leading to a repulsion motivation when individuals get too close to one another. Following this first key rule, cohesion also is important to individual decisions about movement, taking precedence over polarization. As individuals are swimming, group-level cohesion and polarization are largely explained by individual changes in direction and speed based on interindividual distances. In addition, beyond these general rules, the work suggests interesting species-level differences in these movement dynamics. For example, zebrafish grouping seems to be more vertically distributed in water than is the case for black neon tetra. Taken together, this work is significant in that it

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Deceased-Infant Carrying in Nonhuman Anthropoids: Insights From Systematic Analysis and Case Studies of Bonnet Macaques (*Macaca radiata*) and Lion-Tailed Macaques (*Macaca silenus*)

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Existing models of attachment do not explain how death of offspring affects maternal behavior. Previous descriptions of maternal responsiveness to dead offspring in nonhuman anthropoids have not expounded the wide variation of deceased-infant carrying (DIC) behavior. Through the current study, we attempt to (a) identify determinants of DIC through a systematic survey across anthropoids, (b) quantitatively assess behavioral changes of mother during DIC, and (c) infer death perception of conspecifics. Firstly, we performed phylogenetic regression using duration of DIC as the dependent variable. Secondly, we undertook case studies of DIC in the bonnet monkey and the lion-tailed monkey through behavioral sampling. Results of phylogenetic Generalized Linear Mixed Model ($N_{\text{species}} = 18$; $N_{\text{cases}} = 48$) revealed a strong homology ($H^2 = 0.86$). We also obtained a high intraspecific variation in DIC and found DIC to be affected by mother's age, context of death, habitat condition, and degree of arboreality. We found bonnet mothers to carry their deceased offspring for 3.56 ± 4.03 SD days ($N = 7$) with diminished feeding, enhanced passivity, and social isolation during DIC and progressive decline in protection/attentiveness of corpse and attachment. Following Anderson (2016)'s framework of death perception, we interpreted repeated sensory investigation of corpses by mothers as comprehending causality of death, inanimate handling of corpse and its defense as comprehension of non-functionality, and a progressive disinterest of mothers in them as perceiving irreversibility of death. Lastly, we integrated DIC with mother-infant attachment theories and proposed a conceptual model characterizing DIC with causal determinants.

Keywords: deceased-infant carrying, response to death, grief, bonnet monkey, mother–infant attachment

Supplemental materials: <http://dx.doi.org/10.1037/com0000140.supp>

This article was published Online First October 11, 2018.

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We thank Yukimaru Sugiyama, Elizabeth Williamson, Kazukiho Hosaka, Michael Huffman, Patricio Ramírez Llorens, Kawabe Tomohiro, Yamagiwa Juichi, John Kahekwa, Peter Fashing, Baoping Ren, Patricia Izar, Gautam Sharma, and L.S. Rajpurohit for providing additional infor-

mation on their publication reporting deceased-infant carrying. Adwait Deshpande, Shreejata Gupta, and Anindya Sinha also shared their data on three cases of deceased-infant carrying in the bonnet monkey. We also extend our gratitude to Madhur Mangalam for aiding in survey of obscure literature; Mahalakshmi, S. and T. Larimer for sharing their observations; Tejeshwar Dhananjaya for assistance with behavioral observations; Werner Kaumanns for his persistent interest, productive discussion, and guidance in drafting the manuscript; and finally, Sheethal V. R. for assistance in editing the write-up. Sayantan Das is supported by Government of India University Grants Commission fellowship, and Mewa Singh received financial assistance under Science and Engineering Research Board's (Government of India) Jagadish Chandra Bose fellowship scheme.

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Freestanding Bipedal Posture and Coordinated Bimanual Manipulation Significantly Influence Lateralized Hand Use in Rhesus Monkeys (*Macaca mulatta*) and Chimpanzees (*Pan troglodytes*)

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Investigations of behavioral lateralization in nonhuman primates yield important insights into brain–behavior relationships. In turn, they provide clues about both proximal and distal factors that shape the development and expression of association between motor asymmetries and underlying neural substrates. Nonhuman primates afford unique comparative opportunities to evaluate potential routes for the evolution of handedness, as well as to uncover relationships between behavioral lateralization and underlying neural, genetic, and physiological correlates. We examined hand preference in 22 rhesus monkeys and 79 chimpanzees using unimanual reaching tasks varying in postural stability and in a coordinated bimanual task. The majority of rhesus monkeys and chimpanzees showed significant lateral biases when reaching from a freestanding posture and when engaged in a coordinated bimanual task. Population-level directional bias was not evident for any task for rhesus monkeys and was observed only in the bimanual task for chimpanzees. We did not find consistent relationships between an individual's hand preference for different types of tasks. Both freestanding bipedal posture and coordinated bimanual hand use elicited significantly stronger lateral biases in reaching when compared with quadrupedal reaching. These data support the hypothesis that both degrees of postural instability and complex manipulation, such as bimanual coordination, may influence the expression of behavioral asymmetries in primates. These results demonstrate robust lateralization occurs at the individual level. Our results also highlight the need for greater consideration of task type and descriptive data in studies aimed at evaluating brain–behavior relationships and individual differences associated with hand preference.

Keywords: *Macaca mulatta*, *Pan troglodytes*, asymmetry, handedness, laterality

Identifying the extent to which aspects of nonhuman primate lateralized hand use are analogous, or even homologous, to human handedness is of interest at many levels. Among them, the comparative study of human and nonhuman primate handedness may inform understanding of the evolution of cerebral organization, the

interplay between cerebral and behavioral asymmetry, and—ultimately—the factors that influence the development of individual differences in these domains.

The view of nonhuman primate hand preferences as behavioral biases, shaped by the environment without analogy to human

This article was published Online First October 29, 2018.

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We gratefully acknowledge the assistance of Keri Chiodo, Jessica L. Christensen, Jamie Ronchetto, Megan Slocum, and Erin Sullivan in data collection from rhesus monkeys. We appreciate helpful comments and discussion pro-

vided by Peter J. Pierre. We also appreciate the assistance of Keith Groach and Christopher Corcoran in article preparation. Observations with the animals were made in accordance with the Guide for the Care and Use of Laboratory Animals published by the U.S. National Institutes of Health (NIH Publication No. 85–23, revised 2011). The research and article preparation were partially supported by NIH Grants MH084980, AA11997, AA017056, U42-RR15090, NS-42867, HD-38051, and HD-56232.

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Locomotion and Posture Development in Immature Male and Female Rats (*Rattus norvegicus*): Comparison of Sensory-Enriched Versus Sensory-Deprived Testing Environments

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The aim of the current study was to provide normative data on spontaneous locomotion and posture behavior in developing rats (*Rattus norvegicus*), during the first 2 postnatal weeks. Male and female rat pups were tested daily from P1 (postnatal day 1; ~24 hr after birth) to P15 in a sensory-enriched or sensory-deprived testing environment, which was enclosed in a temperature-controlled incubator. Pups in the sensory-deprived condition were tested individually and placed in a square, Plexiglas box (open-field) for a 20-min test period. Pups in the sensory-enriched condition were placed in the same box with the siblings and bedding from the home cage to provide sensory stimulation that mimicked the home nest. Subjects in this condition were tested two at a time, with an additional two siblings (2 males and 2 females total in box). It was hypothesized that pups in the sensory-enriched testing condition would demonstrate more mature patterns of behavior, given the presence of behavior-activating sensory stimuli in the box. It was found that rat pups exhibited spontaneous pivoting and crawling as early as P1, regardless of sensory stimulation present in the testing environment. These behaviors were shown at least 1 to 3 days earlier than reported in prior studies. Quadrupedal walking occurred as early as P4 but was not reliably expressed until P10/11. These findings suggest that controlling temperature during testing influences the typical age of first occurrence of these behaviors. Finally, there were no sex differences in the duration of locomotion and posture behaviors.

Keywords: motor behavior, neonatal rat, environment, temperature, movement

In rats, as with all mammals, the neural mechanisms supporting locomotion begin developing in utero (Bekoff & Lau, 1980; Brumley & Robinson, 2005) and continue developing postnatally (Vinay et al., 2002). Nearly every research article over the last 40 years that has examined the developmental trajectory of locomotion in rats, or how this trajectory may be affected by experimental manipulations, bases developmental time points of emergence of locomotion on a study published by Altman and Sudarshan in 1975. In fact, according to Google Scholar, over 750 articles examining or manipulating the neurobehavioral development of locomotion in rats cites Altman and Sudarshan (1975). In that seminal paper, the age of the first spontaneous occurrence of different forms of locomotion and posture (i.e., limb elevation, pivoting, crawling, head elevation, and walking) in rats are reported in an open-field testing environment. In general, it is reported that posture and locomotion of the upper body (head and

forelimbs) developmentally precedes that of the lower body (hindlimb), as evidenced by pivoting and crawling occurring before full-on quadrupedal walking (Altman & Sudarshan, 1975). The article by Altman and Sudarshan has provided important normative data on locomotion and posture that has enhanced our understanding and knowledge of motor behavior development in a rat model.

However, early studies of locomotion and posture were conducted prior to research that examined physiological processes and development and maturation of body systems. For example, Bolles and Woods (1964) and Altman and Sudarshan (1975) conducted their studies prior to much of the research that examines thermoregulation in newborn rats. Thus, temperature was not a variable that was taken into consideration at the time; both studies conducted testing of immature rats at room temperature. Yet, it is now known that it is necessary to consider ambient temperature during behavioral testing (Harshaw, Blumberg, & Alberts, 2017) because immature rat pups are unable to effectively self-regulate their body temperatures internally for long periods of time. In fact, sensitivity to thermal stress, both acute and chronic exposure, can occur as early as gestation and continues after birth, as newborn rats are inefficient at independent thermoregulation (Blumberg, Sokoloff, & Kirby, 1997; Blumberg & Stolba, 1996; Gordon, 1993; Horwitz, Heller, & Hoffmann, 1982). Newborn rats are capable of using brown adipose tissue (BAT) to produce heat shortly after birth; however, BAT thermogenesis requires the animal to expend high amounts of energy (Cannon & Nedergaard, 2004). Thus, it is

This article was published Online First November 1, 2018.

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This study was supported by an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health under Grant P20 GM103408.

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Like Chimpanzees (*Pan troglodytes*), Pigeons (*Columba livia domestica*) Match and Nash Equilibrate Where Humans (*Homo sapiens*) Do Not

Yosuke Hachiga, Lindsay P. Schwartz, Christopher Tripoli, Samuel Michaels, David Kearns,
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Martin, Bhui, Bossaerts, Matsuzawa, and Camerer (2014) found that chimpanzee pairs competing in matching-pennies games achieved the Nash equilibrium whereas human pairs did not. They hypothesized this outcome may be due to (a) chimpanzee ecology producing evolutionary changes that give them a cognitive advantage over humans in these games, and (b) humans being disadvantaged because the cognition necessary for optimal game play was traded off in evolution to support language. We provide data relevant to their hypotheses by exposing pairs of pigeons to the same games. Pigeons also achieved the Nash equilibrium, but did so while also conforming with the matching law prediction on concurrent schedules where choice ratios covary with reinforcer ratios. The cumulative effects model, which produces matching on concurrent schedules, also achieved the Nash equilibrium when it was simulated on matching-pennies games. The empirical and simulated compatibility between matching law and Nash equilibrium predictions can be explained in two ways. Choice to concurrent schedules, where matching obtains, and choice in game play, where the Nash equilibrium is achieved, may reflect the operation of a common process in choice (e.g., reinforcer maximization) for which matching and achieving the Nash equilibrium are derivative. Alternatively, if matching in choice is innate as some accounts argue, then achieving the Nash equilibrium may be an epiphenomenon of matching. Regardless, the wide species generality of matching relations in nonhuman choice suggests game play in chimpanzees would not prove advantaged relative to most species in the animal kingdom.

Keywords: Nash equilibrium, matching pennies, matching law, chimpanzees, pigeons

Dennett (1983) has suggested that theorizing about mental function levels in humans and other animals is done by two types of researchers, killjoys and romantics. Killjoys place humans at the apex of any ranking of mental function, viewing their mental capacities as unrivaled in the animal kingdom; romantics, on the other hand, often see equivalences in mental function between humans and some other animals.

We have no quarrel with this dichotomy and see the literature on comparative cognition as offering cases in which one or the other view seems sensible and useful. However, there is a small literature that falls *outside* the Dennett's dichotomy. This literature claims to show mental function in chimpanzees that is superior to that seen in humans in terms of short-term memory (Inoue & Matsuzawa, 2007), self-control in intertemporal preferences (Rosati, Stevens, Hare, & Hauser, 2007), and rational maximizing (Jensen, Call, & Tomasello, 2007).

We have opposed these claims, arguing that, in one way or another, they overreach (Genty, Karpel, & Silberberg, 2012; Silberberg & Kearns, 2009; Smith & Silberberg, 2010). These references once challenged all published claims of mental function outside the Dennett's dichotomy of which we were aware; however, matters have recently changed. Martin et al. (2014) offered credible demonstrations that when pairs of chimpanzees or humans make repeated binary choices in competition for reinforcement, chimpanzees come closer to achieving the so-called Nash equilibrium (NE)—a point where each participant in a competitive game cannot gain by a unilateral change in choice strategy if the strategy of the opponent remains unchanged. To familiarize the reader with this work, we summarize their report in the following text.

Martin et al.'s (2014) Procedure and Results

Martin et al. (2014) exposed pairs of chimpanzees, sitting in proximity, to three matching-pennies games in which each subject chose on its own touch screen between illuminated left- and right-side squares. In all games, one member of the pair, the matcher, was rewarded with apple only when it chose the same square on its touch screen as the other member; the mismatcher, on the other hand, was rewarded only when it chose the square opposite that chosen by the matcher.

The payoff structure differed in each game for the matcher: In the 2,000-trial *symmetric game*, matches resulted in a single apple cube; in the 1,000-trial *asymmetric game* that followed, left-side matches yielded three apple pieces and right-side matches yielded

This article was published Online First October 29, 2018.

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This work was funded by National Institutes of Health 1 R15 MH109922 to American University and by Japan Society for the Promotion of Science Overseas Research Fellowships to Yosuke Hachiga.

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Object Permanence in *Giraffa camelopardalis*: First Steps in Giraffes' Physical Cognition

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Although behavior, biology, and ecology of giraffes have been widely studied, little is known about their cognition. Giraffes' feeding ecology and their fission–fusion social dynamics are comparable with those of chimpanzees (*Pan troglodytes*), suggesting that they might have complex cognitive abilities. To assess this, we tested 6 captive giraffes on their object permanence, short-term memory, and ability to use acoustic cues to locate food. First, we tested whether giraffes understand that objects continue to exist even when they are out of sight. Giraffes saw one of two opaque containers containing food, then containers were closed, and 2 s later giraffes could choose one. Second, we measured giraffes' memory repeating the procedure but with a delay of 30 s, 60 s, or 2 min between closing the containers and subjects' choice. Finally, we investigated whether giraffes could locate food inside one of two identical opaque containers, when the only cue provided was the sound made by food when shaking the baited container, or the lack of sound when shaking the empty container. Our results show that giraffes form mental representations of completely hidden objects, but may not store them for longer than 30 s. Moreover, they rely on stimulus enhancement rather than acoustic cues to locate food, when no visual cues are provided. Finally, we argue that giraffes and other ungulates might be a suitable model to investigate the evolution of complex cognitive abilities from a comparative perspective.

Keywords: object permanence, short-term memory, acoustic cues, giraffe, Bayesian statistics

Supplemental materials: <http://dx.doi.org/10.1037/com0000142.supp>

Giraffes are a neglected species in science, with only 400 scientific articles having been written about them, as compared with 20,000 articles on white rhinos, for instance (Dell'Amore,

2016). Besides this, all we know about giraffes is limited to their behavior, biology, and ecology, but nothing is to our knowledge known about their cognition (Dagg, 2014; Seeber, Ciofolo, & Ganswindt, 2012; Shorrocks, 2016). During the past 15 years, the number of wild giraffes has plummeted from an estimated 140,000 to around 9,000, and our limited knowledge about them makes conservation efforts a very difficult task (Muller et al., 2016).

In the wild, giraffes form fission–fusion groups, with individuals joining subgroups of different size and composition, which vary from one individual (usually adult bulls) up to 100. Cows usually form small subgroups with calves and other cows, and the probability and stability of a relationship between two giraffes is determined by kinship and shared space (Bercovitch & Berry, 2013; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Vander-Waal, Wang, McCowan, Fushing, & Isbell, 2014). These fission–fusion social dynamics are thought to be linked to the evolution of complex cognitive abilities, as for example in chimpanzees (*Pan troglodytes*), although subtle differences in fission–fusion dynamics may posit different cognitive challenges across animal taxa (Aureli et al., 2008).

From an ecological point of view, giraffes have a very diverse diet, eating different specific leaves and flowers depending on the time of the year (Berry & Bercovitch, 2017). Indeed, new long-term evidence has shown that giraffes' diet is much more varied than previously thought, and their dietary breadth is comparable

This article was published Online First October 29, 2018.

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We thank the staff at the facilities of Barcelona and Leipzig, Oscar Quilez Peña, Bibiana Martin Prat, Ruben Holland, Rene Forberg, Daniel Volkmann, Kathrin Dorn, Marco Mehner, Stefan Lohmer, Michael Tempelhof, and all the others for endless support and cooperation. We also thank Fred Bercovitch for his clever commentaries on a previous version of this article. Last, we thank Maria Luisa Caicoya for helping us coding all the trials for interobserver reliability. This research was supported by a Programa de Investigación y Conservación (PRIC) grant, convocatoria 2016/2017, Fundación Zoo de Barcelona.

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The Effects of Ambient Temperature and Lighting Intensity on Wheel-Running Behavior in a Diurnal Rodent, the Nile Grass Rat (*Arvicanthis niloticus*)

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Environmental conditions, such as the light–dark cycle and temperature, affect the display of circadian rhythmicity and locomotor activity patterns in mammals. Here, we tested the hypothesis that manipulating these environmental conditions would affect wheel-running activity patterns in a diurnal rodent, the Nile grass rat (*Arvicanthis niloticus*). Grass rats are diurnal in the field, however, a subset switch from a day-active pattern to a night-active pattern of activity after the introduction of a running wheel. The mechanism of this chronotype switch remains largely unknown. In the present study, grass rats were presented with running wheels in 12:12 light–dark conditions. First, subjects were exposed to 25 °C during the day and 21 °C at night, which resulted in 100% of grass rats expressing diurnal behavior. Subjects were then exposed to manipulations of elevated ambient temperature, which resulted in a significant reduction in wheel-running activity. Reducing ambient temperature below 21 °C, however, did not disrupt the expression of diurnality or overall activity. Next, lighting intensity was reduced, which resulted in a switch from a diurnal to a nocturnal chronotype in a subset of animals and reduced overall wheel-running activity. Upon return to baseline lighting intensity, patterns of diurnal activity were restored. Altogether, increases in ambient temperature and decreases in lighting intensity significantly reduced overall wheel-running activity. Importantly, dim light resulted in a temporal niche switch in a subset of grass rats, suggesting a critical role for lighting intensity on the expression of wheel-running activity patterns.

Keywords: temperature, circadian, light, environment, behavior

Environmental conditions influence physiology and behavior in mammals. In most regions on Earth, the cycle of a day brings about the rise and fall of the sun, generating predictable changes in lighting intensity and ambient temperature in nature. Importantly, environmental fluctuations, such as temperature and light, influence the display of circadian rhythms in physiology and behavior in organisms ranging from bacteria to mammals (Pittendrigh, 1993; Reilly, 1990). Light and temperature are important entraining stimuli (i.e., Zeitgebers) for diurnal animals, those that are active during the day (Vivanco, Rol, & Madrid, 2010), and also for nocturnal animals, those that are active at night (Refinetti, 2010).

The timing and intensity of light are powerful entraining stimuli, evoking behavioral and chronotype changes in mammals. Seasonal changes in behavior are significantly affected by changes in lighting intensity (Heldmaier, Steinlechner, Rafael, & Latteier, 1982). In humans, the lack of light in the winter months can induce seasonal affective disorder, which results in episodes of depression (Saeed & Bruce, 1998). In cases of seasonal affective disorder, light intensity treatments have been shown to reduce symptoms, suggesting that increased amounts of light can have a positive effect on behavior (Terman et al., 1989; Wakamura & Tokura, 2001). Likewise, light intensity affects the entrainment of biological rhythms, further emphasizing the role light intensity plays in behavior (Wever, Polásek, & Wildgruber, 1983). The effects of light intensity on behavior also extend to diurnal rodent models. Daytime dim light increases anxiety, evokes physiological changes, and results in depression-like behavior in the diurnal Nile grass rat (Ikeno, Deats, Soler, Lonstein, & Yan, 2016; Leach, Adidharma, & Yan, 2013). In addition, lighting intensity has been shown to affect temporal niche switching in some species (Chiesa, Aguzzi, Garcia, Sarda, & de la Iglesia, 2010; Cohen, Smale, & Kronfeld-Schor, 2010; Doyle, Yoshikawa, Hillson, & Menaker, 2008; Kempinger, Dittmann, Rieger, & Helfrich-Forster, 2009; Mrosovsky & Hattar, 2005) and may also affect the timing of the display of activity in grass rats, a hypothesis we tested here.

In addition to lighting intensity, the ambient temperature of an environment also affects behavior in mammals. Organisms use

This article was published Online First November 5, 2018.

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All experiments were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publication No. 80-23) and were approved by the Institutional Animal Care and Use Committee of Hope College. We thank the Psychology Department at Hope College for their support of this research project. This study was also supported by startup funds to Andrew J. Gall from the Social Sciences Division at Hope College. We also wish to thank Jill VanderStoep for providing statistical advice.

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Perception of the Delboeuf Illusion by the Adult Domestic Cat (*Felis silvestris catus*) in Comparison With Other Mammals

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The comparative study of the perception of visual illusions between different species is increasingly recognized as a useful noninvasive tool to better understand visual perception and its underlying mechanisms and evolution. The aim of the present study was to test whether the domestic cat is susceptible to the Delboeuf illusion in a manner similar to other mammalian species studied to date. For comparative reasons, we followed the methods used to test other mammals in which the animals were tested in a 2-way choice task between same-size food stimuli presented on different-size plates. In 2 different control conditions, overall the 18 cats tested spontaneously chose more often the larger amount of food, although at the individual level, they showed interindividual differences. In the Delboeuf illusion condition, where 2 equal amounts of food were presented on different-size plates, all cats chose the food presented on the smaller plate more often than on the larger one, suggesting that they were susceptible to the illusion at the group level, although at the individual level none of them performed significantly above chance. As we found no correlation between the cats' overall performance in the control conditions and their performance in the illusion condition, we propose that the mechanisms underlying spontaneous size discrimination and illusion perception might be different. In the discussion, we compare the results of the present study with the results for other previously tested mammals and highlight some possible reasons for their similarities and differences.

Keywords: *Felis silvestris catus*, quantity discrimination, spontaneous two-way choice test, visual illusion, visual perception

Supplemental materials: <http://dx.doi.org/10.1037/com0000152.supp>

Many animal species obtain a significant amount of the information about their environment via their visual systems. However, the way this sensory information is captured and processed can vary notably across species. Within vertebrates, even within mam-

mals, these differences originate from anatomical differences in the structure and position of the eyes (Heesy, 2008; Lamb, Collin, & Pugh, 2007; Veilleux & Kirk, 2014) and their underlying neural circuits (Eagleman, 2001; Mascalzoni & Regolin, 2011; Masland & Martin, 2007), both shaped by evolutionary processes. However, the visual assessment of a target object, for example, its color, shape, or size, can be distorted by the surrounding environment, leading to so-called visual illusions (Gregory, 1997).

Humans have long been known to perceive a wide range of optical illusions (Wade, 2017), and the comparative study of illusions between humans and nonhuman mammals is increasingly recognized as a noninvasive tool to better understand visual perception and its underlying mechanisms and evolution. Comparative studies have revealed both similarities and differences in susceptibility to geometrical visual illusions (pertaining to an object's size and shape) across species. It seems that, in general, most animals are susceptible to at least some geometrical optical illusions (e.g., 11 of 13 tested vertebrate species have been found to be susceptible to the Ponzo and Müller-Lyer illusions in the same manner as humans; Byosiére, Feng, Rutter, et al., 2017; Byosiére et al., 2018; review in Feng, Chouinard, Howell, & Bennett, 2017), albeit with some notable differences. In contrast, in the case of the Ebbinghaus illusion, which has been amply studied in a variety of species with different ecological and taxonomical backgrounds, no discernible pattern is apparent in susceptibility to the illusion or the direction in which it is perceived

This article was published Online First November 5, 2018.

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Financial support was provided by a research grant from the Universidad Nacional Autónoma de México (UNAM; DGAPA-IN205513) and by a postdoctoral fellowship from the Instituto de Investigaciones Biomédicas, UNAM to Oxána Bánszegi, and by a student grant from the Consejo Nacional de Ciencia y Tecnología, Mexico, to Andrea Urrutia. We thank Carolina Rojas for excellent technical and bibliographical assistance, undergraduate student Sandra Martínez-Byer for help with testing and cat management, and cat owners Francisco Javier Chang Castellanos, Esther Garcilita, Zita Groó, Irene Urrutia, David Ramírez Ortiga, Karina Isabel Ángeles Ortiz, and Giomara Cabrera Tercero for allowing us repeated access to their homes and cats. We also thank Royal Canin® for supporting our research.

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Associations Among Behavioral Inhibition and Owner-Rated Attention, Hyperactivity/Impulsivity, and Personality in the Domestic Dog (*Canis familiaris*)

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In humans, behavioral disinhibition is associated with attention-deficit/hyperactivity disorder (ADHD). Limitations to rodent models of ADHD-like behaviors/symptoms may be augmented by complementary ones, such as the domestic dog. We examined associations between family dogs' ($N = 29$; of 14 breeds and 12 mongrels) performance on a self-developed touchscreen behavioral Go/No-Go paradigm and their owner-rated inattention and hyperactivity/impulsivity, accounting for relevant covariates. A greater proportion of commission errors was associated with greater hyperactivity/impulsivity. Regardless of accuracy, relative to dogs with no previous training, those with basic training had shorter response latencies. Also, regardless of accuracy, greater confidence and extraversion were associated with shorter latencies, and greater openness was associated with longer latencies. Shorter latency to commission errors was associated with greater inattention. Findings support the dog as a model of the association between behavioral disinhibition and ADHD-like behaviors/symptoms and are early evidence of convergent validity between the behavioral paradigm and the rating scale measure in dogs.

Keywords: behavioral inhibition, inattention, hyperactivity/impulsivity, domestic dog, Go/No-Go test

Supplemental materials: <http://dx.doi.org/10.1037/com0000151.supp>

In the cognitive and/or neuropsychology literatures, behavioral or response inhibition is the ability to suppress actions that are inappropriate or undesirable, given short-term adaptation and long-term goals (Barkley, 1997; Castellanos, Sonuga-Barke, Milham, & Tannock, 2006; Nigg, 2001). Specifically, behavioral inhibition is definable as “three interrelated processes: (a) inhibition of an

initial, prepotent response to an event (inhibitory control); (b) stopping of an ongoing response, which thereby permits a delay in the decision to respond; and (c) the protection of this period of delay and the self-directed responses that occur within it from disruption by competing events and responses (interference control)” (Barkley, 1997, p. 67). The first two of these processes are

This article was published Online First November 5, 2018.

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We thank all dogs (*Akina, Alma, Barka, Bingó, Bogyó, Borisz, Demi, Dolores, Döme, Joker, Kitty, Kópé, Leia, Lili, Liza, Lizi, Lord, Lucky, Mara, Molly, Monty, Öre, Pille, Rozi, Rynn, Simon, Vackor, Zajec, Zebulon*) and their owners for their participation in our trainings and test and owners for completing our questionnaires. We thank Rita Báji for her assistance. This research was funded by the National Research, Development and Innovation Office (Grant 115862K) and the Hungarian Academy of Sciences (Grant F01/031). During the preparation of this article, Nóra Bunford was also funded by the MTA Premium Postdoctoral Fellowship

(PREMIUM-2017-67) and by the New National Excellence Program, 2017/2018 (ÚNKP-17-4-ELTE/12423/11).

Nóra Bunford contributed toward conceptualization, formal analysis, writing—original draft, writing—review and editing, and visualization; Barbara Csibra toward conceptualization, methodology, investigation, writing—review and editing, and project administration; Csenge Peták toward investigation, software, and writing—review and editing; Bence Ferdinandy toward software and writing—review and editing; Ádám Miklósi toward writing—review and editing and funding acquisition; and Márta Gácsi toward conceptualization, methodology, resources, writing—review and editing, supervision, and funding acquisition.

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Social Learning of Goal-Directed Actions in Dogs (*Canis familiaris*): Imitation or Emulation?

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A goal-directed action is composed of two main elements on which the observer may focus its attention: the movement performed (i.e., the action) and the outcome (i.e., the goal). In a social learning situation, consequently, the observer may imitate the action of the model or emulate the result of its action. In humans and primates, the tendency to selectively engage in any of these two processes is considered to be dependent upon the availability and saliency of information about the goal, implying the capacity to recognize the goals of others' actions. Dogs are skillful in learning socially from humans, and, when trained with the Do as I Do method, they imitate human actions. Here, we tested trained dogs for engaging in imitation or emulation based on information about the goal. We found that dogs observing the demonstration of an object-related action in the absence of a clear goal tended to solve the task by matching the body movement of the human demonstrator. In contrast, when they could observe the exact same movement, but the goal was apparent, they attempted to solve the task by their own means, that is, by emulation, instead of imitating the demonstrated action. These results provide experimental evidence for dogs being able to recognize the goals of others and adjust their behavior accordingly, relying flexibly on imitation or emulation.

Keywords: imitation, emulation, dog, goal-directed action, social learning

Supplemental materials: <http://dx.doi.org/10.1037/com0000149.supp>

The demonstration of goal-directed actions contains two main observable sources of information: a movement or motor part and a consequence or effect that is the goal of the action (Elsner, 2007). A goal is defined as an observable, physical end-state or outcome (Leighton, Bird, & Heyes, 2010; Wohlschläger, Gattis, & Bekker-

ing, 2003). Emulation is the process by which an observer, by watching a model, learns about the results of its actions—that is, the goals—rather than the details of the behavior involved (Horner & Whiten, 2005; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Therefore, in emulation only the end-state of what the model has done is copied (Tomasello & Call, 1997; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009; Wood, 1989). By imitation, in contrast, the observer learns some specific aspects of the intrinsic form of the act from the observation of the model (Whiten & Ham, 1992). Thus, apart from vocal imitation, it is the orientation and the shape of the action—that is, the action in terms of movements performed—that is attended to and reproduced when imitating (Horner & Whiten, 2005).

Whether human infants represent the goals and intentions of others has been the focus of many empirical studies (Meltzoff, 1995; Olineck & Poulin-Dubois, 2009; see also Elsner, 2007 for a review). Human infants' sensitivity to goal-directed actions is apparent already from the first year of their life (Hamlin, Hallinan, & Woodward, 2008; Thoermer, Woodward, Sodian, Perst, & Kristen, 2013), and they are generally considered to encode the object-related actions of others in terms of their goals from this early age (Gergely, Nádasdy, Csibra, & Bíró, 1995; Meltzoff, 1995; Robson & Kuhlmeier, 2016; Woodward, 1998).

This article was published Online First November 8, 2018.

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This study was supported by the National Brain Research Program (2017–1.2.1-NKP-2017–00002). Claudia Fugazza also received a grant from Association of Professional Dog Trainers. A.P. was supported by the ÚNKP-17–4 New National Excellence Program of the Ministry of Human Capacities, Hungary and by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Ádám Miklósi received funding from MTA-ELTE Comparative Ethology Research Group (MTA01 031). We are grateful to the dog owners that participated with their dogs in this study.

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Personality in Captive Killer Whales (*Orcinus orca*): A Rating Approach Based on the Five-Factor Model

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The comparative study of animal personality has received great interest in recent years. Some studies have analyzed personalities in cetaceans (exclusively in dolphins), but none have analyzed the factorial structure of personality of any species in this order. Our objective was to evaluate a sample of captive killer whales ($n = 24$) adapting one of the most widely used models of personality in humans and nonhuman animals: the five-factor model. A total of 38 personality descriptive adjectives were rated by 55 raters (mainly trainers and curators). Principal components analysis and regularized exploratory factor analysis revealed four statistically significant factors with acceptable standards of interrater reliability and validity, accounting for 49.85% of the variance. The first factor indicated an Extraversion factor, the second one revealed a combined factor of Conscientiousness and Agreeableness, the third one yielded in a Dominance factor, and the fourth one reflected a Careful factor very close to a combination of Conscientiousness and Agreeableness factor. The results were compared with the results obtained for humans and chimpanzees in prior studies. The similarities could be explained as a result of convergent adaptive traits despite a deep evolutionary divergence, adaptation to physically dissimilar environments, and very different neuroanatomical organization.

Keywords: killer whale, orca, personality, temperament, five factor model

Supplemental materials: <http://dx.doi.org/10.1037/com0000146.supp>

Studies investigating personality in nonhuman animals have been carried out over a wide range of species (see Gosling, 2001 and Carere & Maestriperi, 2013, for review). The species studied

range from invertebrates, such as mollusks and arthropods, to vertebrates, such as amphibians, reptiles, birds and fish, but the majority of studies examined personality in mammals. Regarding cetaceans, personality studies have been carried out exclusively in dolphins. Those studies have documented individual differences that remain consistent over time (Highfill & Kuczaj, 2007) and across contexts (Highfill & Kuczaj, 2010; Kuczaj, Highfill, & Byerly, 2012). Moreover, it has been documented how individual differences can predict neophilia (Skrzypczak, 2016) for the Atlantic spotted dolphin (*Stenella frontalis*) and how these differences play a role in various social contexts including play behavior (Kuczaj & Eskelinen, 2014), social rank (Frick, 2016; Highfill & Kuczaj, 2010), learning (Kuczaj, Yeater, & Highfill, 2012), and bonds (Birgersson, 2011; Moreno, 2017) for bottlenose dolphins (*Tursiops truncatus*). However, none of these studies have analyzed the factor structure of personality for the species by using data reduction. The current study examines the personality structure of a previously unstudied cetacean, the killer whale (*Orcinus orca*).

The study of animal personality has been approached from very different perspectives, including to analyzing the structures of

This article was published Online First November 15, 2018.

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We thank Loro Parque Foundation's grant (SS-116-2016-1) for providing funding for this research. We also thank Loro Parque and SeaWorld for their facilities in order to complete this project and all the raters for helping in the personality questionnaire assessment. Thank you to our editor and reviewers for their constructive and detailed feedback, and to Sharon Rose for the English revision of this article.

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Preference for Attractive Faces Is Species-Specific

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Studies on facial attractiveness in human adults, infants, and newborns have consistently reported a visual preference for faces rated as attractive compared with faces rated as unattractive. Biological accounts of facial attractiveness have typically presented such preferences as arising from adaptations for mate choice or as by-products of general sensory bias. In this cross-species study, we examined whether explicit ratings of attractiveness made by human judges would predict implicit visual preferences in other humans and also in rhesus macaques and, if they do, whether such preferences would extend beyond conspecific faces. Results showed that human ratings of attractiveness can predict implicit preferences in nonhuman primates (macaque monkeys; *Macaca mulatta*). However, we also found a species-specific effect of face attractiveness in which humans showed a visual preference for human faces (but not macaque faces) rated as attractive, and macaques displayed a visual preference for macaque faces (but not human faces) rated as attractive. Overall, the findings suggest that attentional bias toward attractive faces arises neither from an exclusive operation of mate choice adaptation mechanisms nor from the sole influence of a general sensory bias, but rather reflects their interaction. The influence of a general sensory bias may be modulated by the categorization of a face as conspecific or heterospecific, leading to species-specific preference for attractive faces.

Keywords: humans, rhesus macaques, faces, attractiveness, eye-tracking, mate choice

Supplemental materials: <http://dx.doi.org/10.1037/com0000148.supp>

Despite the long held view that “beauty is in the eye of the beholder,” judgments of facial attractiveness are largely shared both within and between cultures (Cunningham et al., 1995; Jones

& Hill, 1993; Langlois et al., 2000; Little, Jones, & DeBruine, 2011; Perrett et al., 1998; Perrett, May, & Yoshikawa, 1994; Rhodes, 2006; Rhodes et al., 2001). While acknowledging inter-observer variation (Hönekopp, 2006), multiple reports indicate that there can be a common sensibility of what is attractive across cultures and point to a biological account of the preference for attractive faces (Hahn & Perrett, 2014; Little et al., 2011; Rhodes, 2006).

Facial attractiveness is influenced by a variety of factors (for a review and a meta-analysis, see Little et al., 2011; Rhodes, 2006), eluding explanation by a single principle. Due to this multifactor determination, physical measurements of attractiveness are not straightforward as are, for example, height or weight measures. The easiest and most common way to evaluate beauty in a face is to ask human observers to rate a face for its attractiveness. These explicit judgments of attractiveness are a good predictor of implicit behaviors linked to preferences, such as longer looking times, either in adults (Hayden, Parikh, Deaner, & Platt, 2007; Leder, Tinio, Fuchs, & Bohrn, 2010; Shimojo, Simion, Shimojo, & Scheier, 2003), or in infants from 2- to 3-day-olds to 15-month-olds (Damon, Méary, et al., 2017; Damon, Mottier, Méary, & Pascalis, 2017; Langlois, Ritter, Roggman, & Vaughn, 1991; Langlois et al., 1987; Samuels, Butterworth, Roberts, Graupner, & Hole, 1994; Samuels & Ewy, 1985; Slater, Quinn, Hayes, &

This article was published Online First December 13, 2018.

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We thank Annika Paukner for sharing pictures of rhesus macaque faces, and Mike Burt for sharing pictures of human faces. This research was supported by the Open Research Fund of the State Key Laboratory of Cognitive Neuroscience and Learning, and the National Natural Science Foundation of China (Grant 91432102).

R code and raw data are available at: <https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Ftq8bg%2Fdownload>.

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Timing of Antisynchronous Calling: A Case Study in a Harbor Seal Pup (*Phoca vitulina*)

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Alternative mathematical models predict differences in how animals adjust the timing of their calls. Differences can be measured as the effect of the timing of a conspecific call on the rate and period of calling of a focal animal, and the lag between the two. Here, I test these alternative hypotheses by tapping into harbor seals' (*Phoca vitulina*) mechanisms for spontaneous timing. Both socioecology and vocal behavior of harbor seals make them an interesting model species to study call rhythm and timing. Here, a wild-born seal pup was tested in controlled laboratory conditions. Based on previous recordings of her vocalizations and those of others, I designed playback experiments adapted to that specific animal. The call onsets of the animal were measured as a function of tempo, rhythmic regularity, and spectral properties of the playbacks. The pup adapted the timing of her calls in response to conspecifics' calls. Rather than responding at a fixed time delay, the pup adjusted her calls' onset to occur at a fraction of the playback tempo, showing a relative-phase antisynchrony. Experimental results were confirmed via computational modeling. This case study lends preliminary support to a classic mathematical model of animal behavior—Hamilton's selfish herd—in the acoustic domain.

Keywords: rhythm, vocal communication, synchrony, selfish herd, timing

Supplemental materials: <http://dx.doi.org/10.1037/com0000160.supp>

Precise timing of signals is an important dimension in animal communication. Studies on temporal structure have historically focused on individual timing. In contrast, timing can play a role in group interaction by coordinating calls between different individuals (Wilson & Cook, 2016). Across animal species, mechanisms for call timing are often shaped by the species' socioecology (Greenfield & Roizen, 1993; Mathevon, Casey, Reichmuth, & Charrier, 2017). In some species, individuals adjust their timing to vocalize before nearby conspecifics and increase their conspicuousness (Greenfield & Roizen, 1993). Other species show forms of contagious calling (reacting to conspecifics' calls), full synchronization, partial overlap, antisynchrony, and so forth (Ravignani, Bowling, & Fitch, 2014). In particular, antisynchrony consists of

an animal adjusting its next call onset to be a fraction of the previous calling period of the conspecific (Hamilton, 1971; Ravignani, 2014).

Harbor seals are very vocal in the first few weeks after birth (Sauvé, Beuplet, Hammill, & Charrier, 2015). During this time, seal pups live in large mother–pup groups; there, pups call to be noticed by adult females (Perry & Renouf, 1988). Calling concurrently in large groups poses a strategic problem: Many calls at approximately the same time can acoustically mask each other. Individual seal pups could solve this problem of overlap by adjusting the timing of their call onset. Such call adjustment would allow an animal to maintain conspicuousness, if it avoids overlap with a neighbor, and hear the neighbor more clearly (Grafe, 1999; Greenfield, 2015).

In harbor seals, a vocally flexible species (Ralls, Fiorelli, & Gish, 1985), call timing is relevant to understanding the dynamics of communication in a potentially crowded dimension: time. Here, I test the hypothesis that a harbor seal pup possesses timing capacities enabling antisynchronous alternation (Hamilton, 1971; Ravignani, 2014). In other words, I hypothesize the time lag between focal and conspecific call onsets to be a fraction of the conspecific's previous interonset interval (IOI). This is equivalent to an IOI-adjusted lag, that is, a constant phase, so that the focal animal's onset avoids overlap with the conspecific. If so, the expected acoustic outcome in a chorus of harbor seal pups would be antisynchronous alternation of calls over time.

Before the experiment, computational models served to understand behavioral mechanisms underlying seals' timing (Greenfield & Roizen, 1993). Alternative hypotheses (Table S1 in the online supplemental materials) were explored by simulated agents that

This article was published Online First December 13, 2018.

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The author was supported by FWO Pegasus² Marie-Curie fellowship 12N5517N. The author thanks Marianna Anichini, Daryll Carlson, Peter Cook, Bart de Boer, Marianne de Heer Kloots, Koen de Reus, Maxime Garcia, Michael Greenfield, Henkjan Honing, Sonja Kotz, Alice Lowry, Massimo Lumaca, Nicolas Mathevon, Margarita Mendez-Arostegui, Ana Rubio-Garcia, Anna Salazar-Casals, Ruth Sonnweber, Marlene Sroka, for advice, support, and valuable criticism on the manuscript. Data collection was noninvasive and followed the Belgian, Dutch, and EU legislation, and the guidelines for the Association for the Study of Animal Behavior.

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