



With a little help from her friends (and family) part II: Non-maternal caregiving behavior and physiology in mammals

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ABSTRACT

The diversity of competing frameworks for explaining the evolution of non-maternal care in mammals (Part I, this issue) reflects the vast range of behaviors and associated outcomes these theories attempt to subsume. Caretaking comprises a wide variety of behavioral domains, and is mediated by an equally large range of physiological systems. In Part II, we provide an overview of how non-maternal care in mammals is expressed, the ways in which it is regulated, and the many effects such care has on both recipients and caretakers. We also discuss the two primary ways in which closer integration of ultimate and proximate levels of explanation can be useful when addressing questions about non-maternal caretaking. Specifically, proximate mechanisms provide important functional clues, and are key to testing theory concerning evolutionary tradeoffs. Finally, we highlight a number of methodological and publication biases that currently shape the literature, which provide opportunities for knowledge advancement in this domain going forward. In this conclusion to our two-part introduction, we provide a broad survey of the behavior and physiology that the contributions to this special issue represent.

1. Introduction

As discussed in Part I of our introduction to this special issue [1], there are significant challenges associated with finding governing rules amidst the wide variety of ecologies and social systems that mammalian non-maternal care appears in. Herein lies the value of a closer integration of research programs that combine the complementary lessons from proximate and ultimate levels of explanation. Physiological mechanisms can provide important insights on the ultimate function(s) of behavior. Subsets of certain fields, especially research on endocrinology and direct care among mammals, have forged clear and productive pathways in this arena. However, physiology is far broader than hormones, and caretaking consists of a much wider variety of behaviors than the type of “hands-on” care that most physiological research addresses. Our ability to measure physiological parameters has grown alongside our increasingly sophisticated understanding of the diversity of types of care offered, and who it is offered by, but proximate and ultimate integration has not necessarily kept pace.

There are two principle ways in which physiological mechanisms can inform our understanding of the ultimate drivers of observed behaviors. First, the specific patterns we observe in the physiological data

can provide clues about the ultimate function(s) of a behavior. One oft-cited example is the difference in hormone profiles associated with different types of paternal care in humans, rodents, and non-human primates. Which hormones change, and in what direction, hold important clues about the functional significance of the associated behaviors [2–4]. If the primary evolutionary driver in a given species is protection or provisioning, that may be associated with e.g. increased testosterone levels, which may facilitate better performance during conflict or hunting [5–7]. Alternatively, if the primary function is assisting mothers via direct care, that may be associated with increases in prolactin and oxytocin, which facilitate affiliative interactions [8–12].

While endocrine data are regularly invoked for such purposes, other physiological processes are far less commonly used to make inferences about the ultimate functions of behavior. Autonomic nervous system responses, metabolic allocations, and neural activation shifts (to name just a few) hold similar clues, but are much less likely to appear in literature focused on ultimate levels of explanation. While many mechanistic papers allude to the potential fitness implications of a finding, results are more rarely integrated into any specific evolutionary framework that considers cost-benefit tradeoffs (but see e.g. [13–15]). Conversely, much of the work focused on ultimate processes assumes

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costs or benefits, with less attention to the specifics of the physiological processes that underlie such tradeoffs (but see e.g. [16–18]).

This point underpins the second contribution physiological data can make to ultimate research, which lies in the costs and benefits physiological states or changes have for organisms. All currently relevant theoretical frameworks for explaining the evolution of mammalian non-maternal care rely on cost-benefit tradeoffs in some form. Since physiological processes are perhaps the one common currency that all forms of mammalian non-maternal care share despite their extreme socioecological variation, the power of the contributions proximate-level research can make in this area should not be underestimated. Measuring these costs and benefits [6], and establishing concrete connections to their fitness implications [16], is an important and under-explored frontier in the caretaking literature.

In the behavioral ecology literature, costs and benefits are often reduced to gross measures of survival or body size. While these are clearly important considerations, existing frameworks and analyses could expand further to include more nuanced physiological and epigenetic benefits (or costs) accrued by young who receive non-maternal care, and the caregivers who provide it (for examples from the maternal care literature see [19–22]). For instance, experimental work has demonstrated that mouse pups reared in communal nests have greater neural plasticity than counterparts raised in single nests (reviewed in [23]). If neural plasticity confers fitness benefits in the wild (via, perhaps, better problem-solving abilities), then this suggests that 1) selection may have favored communal rearing for reasons beyond simple thermoregulation, or 2) a behavior that originated as a social way to solve an environmental problem had a secondary implication that may have itself had important fitness consequences. Either alternative generates important ultimate-level insights.

Inevitably, some of the lack of integration is due to methodological constraints. Not all systems lend themselves equally well to every question, especially questions that currently require invasive approaches. However, there is much to be gained (including novel methodological contributions, e.g. [24]) from communication between the subset of scientists who are able to carefully study physiological processes in the lab, and those whose field observations shed light on the constraints and advantages of various species' socioecologies. The realities of the publishing system, including the highly-specialized vocabularies that are used in different subsets of the literature, mean they are frequently siloed from each other.

In the remainder of this introduction, we will give an overview of the types of behaviors non-maternal caretakers engage in, the ways in which these behaviors are mechanistically regulated, and the physiological consequences they have for caretakers, recipients, or both. While this review is far from exhaustive, given the size of the bodies of literature it spans, we hope that condensing representative information into a single bibliography will prove useful for those who are interested in finding more specific information about a given subset of the topic (s). We have also made an effort to minimize the use of field-specific jargon, to facilitate ease of reading across a range of disciplines.

2. How is non-maternal care expressed in mammals?

Broadly, caretaking behaviors can be categorized as either direct care (which involves physical touch or direct transfer of resources from the caretaker to the recipient; Table 1a), or indirect (which does not involve overt social interaction between the two, but nonetheless conveys benefits to the care recipient; Table 1b). It is important to note that care does not necessarily constitute investment. A caretaking behavior is only investment if it carries costs for the organism that performs it [25]. There are various types of care, both direct and indirect, that do not necessarily have meaningful costs for the performer [26]. For purposes of this multi-taxa review, we do not distinguish between care and investment; a single behavior may constitute care but not investment in one species, and both in another.

Whether a behavior occurs in a given taxa is dependent on a multitude of factors, but two very basic considerations that govern much of the distributional imbalance are achievability and impact. That is, can the organism achieve it (e.g., carrying behavior would be quite surprising in a ungulate), and what purpose would it serve (e.g., sugar glider joeys may need help thermoregulating, while whale calves do not)? Scientific understanding of the occurrence and distribution of different behaviors is likely to be highly biased by practical and methodological limitations. Behaviors that are discrete and easily identifiable, such as infant transport or allonursing (where a female nurses young that are not her own) are probably much more likely to be both reported and quantified than behaviors which are harder to define or observe (e.g. social facilitation or protection). Species which are large, diurnal, terrestrial, and relatively stationary are usually better-studied than their smaller, nocturnal, marine, or migratory counterparts. Types of care or investment that happen outside the infancy stage are also perhaps less likely to be detected and quantified, even though they may have important fitness ramifications (e.g. [27]). These selection biases may mean that both the range of behaviors, and the range of species in which they occur, is considerably larger than we realize.

One important component of bias in the literature is the primacy of focus on direct care, rather than indirect. While direct care is undoubtedly important, there are many components of it that may have only minor consequences for evolutionarily salient outcomes, especially when any direct care that is offered is a supplement to services offered by mothers (e.g. grooming). Indirect care, especially protection and provisioning (but see also [27]), may have extreme consequences for survival and reproductive outcomes, and have important physiological mediators (e.g. [28]). The focus and volume of the literatures on direct and indirect care do not necessarily reflect the biological realities of the importance of each type to evolutionary dynamics. Rather, they reflect our current methodological limitations and anthropocentric prioritization of behaviors that we can easily see, and perhaps, relate to.

3. How is non-maternal care regulated?

The physiological correlates of caretaking behavior – which may or may not be causal – include endocrine, neural, autonomic, metabolic, immunological, and epigenetic processes. These are not limited to either the caretaker or the recipient; in many cases, both undergo important changes, highlighting the bi-directional nature of these relationships and their evolutionary implications. As with behavior, there are clearly selection biases at work that impede a full understanding of both the range and distribution of physiological processes associated with non-maternal care. Far more is known about the correlates of care in humans and in animal species that are easy to house in laboratories (e.g. mice, marmosets), than about similar processes in species that are more difficult to keep in captivity.

There is a particular dearth of physiological data from social carnivores (but see [8,29–31]), though methodological advances may permit more widespread collection in the near future. Social carnivores are of particular interest in this arena because they are ecological outliers among the mammalian species in which non-maternal care occurs. They occupy a particularly challenging resource acquisition niche that involves extended periods of nutritional stress, followed by short bursts of caloric surplus. Additionally, their high-protein diets may modulate the growth/maintenance and reproduction tradeoffs that all organisms make [32]. This means that the costs and benefits of various behavioral strategies and physiological processes could be different in social carnivores than in their rodent and primate counterparts.

3.1. Bi-directional effects

Though we review the physiological correlates of non-maternal caretaking first in caretakers (Section 3.2), then in care recipients

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