INTRODUCTION



Introduction to topical collection "Measuring individual reproductive success in the wild"

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Published online: 9 August 2022

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Studies of individual reproductive success in wild animals are critical for many aspects of behavior, ecology, evolution, and conservation, including population dynamics, wildlife management, and the possible effects of natural and artificial selective pressures. This Topical Collection tackles the problem of measuring individual reproductive success in the wild, which is often the best approximation of fitness. However, as discussed by Viblanc et al. (2022), how and when reproductive success is measured can lead to different conclusions about the impacts of putative selective pressures. Fortunately, our ability to measure individual reproductive success in the wild has increased substantially in the past few decades, thanks mostly to long-term studies of marked individuals (Clutton-Brock and Sheldon 2010) and new molecular techniques that reveal genetic relationships between parents and offspring. Most of the studies in this Topical Collection span many years, often decades, and use DNA to determine reproductive outcomes.

This Topical Collection seeks to provide an update on studies of individual reproductive success in the wild, and to identify continuing challenges. These studies continue to be mostly limited to mammals and birds, likely because of the logistical challenges of associating parents and offspring in species where propagules such as eggs and larvae are difficult to find and associate with at least one parent, or where it is impossible to extract

This article is a contribution to the Topical Collection Measuring individual reproductive success in the wild. Guest Editors: Janet Mann and Marco Festa-Bianchet.

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a sample for genetic analyses from propagules without killing them. In many taxa, other than mammals or birds, newborn offspring cannot be marked, limiting research on survival to measuring clutch size. Although many studies have genetically assigned offspring to mothers and fathers in amphibians and reptiles (Lee et al. 2022), very few have monitored offspring after they leave the nest or laying site. Similarly, the availability of fitness data for fishes and most invertebrates is sparse, with significant exceptions highlighted in this issue, such as the sponge-dwelling goby (Francis et al. 2022).

For most species, male reproductive success is less wellquantified than female reproductive success, due to considerable challenges identified in this collection (Curren et al. 2022; Foroughirad et al. 2022; Montana et al. 2022; Viblanc et al. 2022). There are some exceptions, such as primate groups where extra-group paternities are rare or absent (Wikberg et al. 2022). Female reproductive success can generally be measured by observation or DNA samples from a mother and her clutch, brood or litter, without sampling other potential mothers. Notable but rare exceptions include species with egg dumping or multiple, hidden clutches within a season. In contrast, paternity assignment requires DNA samples from all possible fathers, and a reliable measure of individual male success requires sampling all possible mates and their offspring. Furthermore, males are sampled at lower rates for a host of reasons: influx of males during seasonal breeding provides a small window of opportunity for sampling; males may range more widely than females and are difficult to locate; males have higher mortality than females and die before sampling can occur; in many species, males disperse. For behavioral ecology, the key issue for inaccurate or incomplete estimates of male reproductive success is whether those estimates are biased with respect to some male characteristics that could affect the interpretation of results (Archer et al. 2022). For example, in bottlenose dolphins, fathers tend to be older than mothers, so those who sired young in their late 20 s and 30 s are often deceased by the time their putative offspring are sampled (Foroughirad



et al. 2022). This is especially evident in the first decades of long-term study because older offspring who are sampled are more likely to have living mothers than living fathers.

The Topical Collection reports many important advances in our understanding of what drives individual reproductive success in the wild. For example, well-established male dominance relationships are often thought to correlate strongly with reproductive success, but studies on spotted hyenas (Curren et al. 2022), white-faced capuchins (Wikberg et al. 2022) and eastern grey kangaroos (Montana et al. 2022) reveal a tenuous correlation due to complexities of social living. In capuchins, subordinate males sometimes had similar reproductive success to the long-term alpha male because alpha males avoid mating with their mature daughters (Wikberg et al. 2022). In sponge-dwelling gobies, size had a positive effect on male reproductive success, but explained little of the variance (Francis et al. 2022). On the other hand, plumage traits related to dominance have a positive effect on the success at obtaining extra-pair paternities in lark buntings, even though females resisted these matings (Lyon and Chaine 2022).

The papers in this collection show that many other factors affect reproductive success, including age and the ability to accumulate resources. Life history parameters impact fitness measurements, especially when reproductive success is strongly age-dependent (Foroughirad et al. 2022; St. Lawrence et al. 2022), or when measuring offspring survival rather than production. These patterns can be sex-specific. In marmots, reproductive success increases towards prime age for both sexes, but in senescence declines more rapidly for males than for females (St. Lawrence et al. 2022). The timing of dispersal decisions for white-faced capuchins (Wikberg et al. 2022) and spotted hyenas (Curren et al. 2022) had considerable impact on male breeding success. Viblanc et al. (2022) find that the apparently beneficial effects of early emergence from hibernation in ground squirrels weaken as one measures reproductive success in ages closer to first reproduction.

Resource acquisition is also important. In red squirrels, food caches are an important resource necessary for reproduction, and have a stronger positive effect on reproductive success of males than of females (Haines et al. 2022). Large sponge-dwelling gobies acquire larger sponges for nesting, that could influence offspring survival (Francis et al. 2022).

Multiple paternity within the same clutch or litter is widespread in amphibians and reptiles. Although it is often inferred that such genetic diversity benefits females, this is true only for salamanders, among the 7 clades with 184 populations of amphibians and reptiles that were examined (Lee et al. 2022). Because males cannot coerce female salamanders to accept spermatophores, the authors suggest female choice is critical to the relationship between polyandry and fitness.

Consistent themes in this collection are that our understanding of lifetime reproductive success remains incomplete without accounting for sex-specific strategies, sexual conflict, timing of life-history events, resource and social competition, and how we measure reproductive success. Comparative analysis across taxa can identify critical and testable hypotheses. Finally, studies spanning the lifetimes and often generations provide both a nuanced and definitive picture of reproductive success in the wild.

Declarations

Conflict of interest The authors declare no competing interests.

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