Age-Specific Forced Polymorphism: Implications of Ontogenetic Changes in Morphology for Male Mating Tactics*

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ABSTRACT

Age-specific forced polymorphism is the presence of two or more distinct phenotypes (here we consider only males) that occur in separate sexually mature age groups (e.g., horns in older males but not younger males). The life-stage morph maturation hypothesis posits that all younger males that possess a particular structure can transform into older males with a different structure, most likely via the influence of hormones. The life-stage morph selection hypothesis posits that polymorphism is due to intense selection resulting in a highly nonrandom sample of younger males surviving to become older males, thus leading to different mean phenotypes in different age groups. We conducted an extensive review of literature from the past 20 years (1983–2003) for cases of age-specific forced polymorphism. Overall, we found only a few cases that fit our criteria of age-specific forced polymorphism, and we argue that most (e.g., orangutans, elephant seals) have likely arisen via the life-stage morph maturation mechanism, but we also present several examples (e.g., green anole lizards) that appear to be candidates for life-stage morph selection. However, none of the reviewed studies provided enough information (e.g., age of morphs, growth patterns of the morphological structure) to definitively invoke either of the two mechanisms. We suggest that age-specific forced polymorphism is more common than reflected in this review and that future studies should gather demographic and laboratory data that will directly compare the life-stage morph maturation and life-stage morph selection hypotheses.

Introduction

Polymorphism, defined as the presence of distinct morphological forms within a particular age/sex class (e.g., males), is well documented in a variety of vertebrate and invertebrate species, including fish, lizards, and beetles. These polymorphisms can take several forms (reviewed in Andersson 1994; Skulason and Smith 1995; Gross 1996; Brockmann 2001; Shuster and Wade 2003; West-Eberhard 2003; Zamudio and Sinervo 2003). For example, Gross (1996) considered three primary forms of polymorphism ("alternative," "mixed," and "conditional" strategies). Alternative strategies are characterized by genetic differences among morphs that each have similar fitness. In turn, these alternative morphs may also exhibit different behavioral tactics or phenotypes. One example of the alternative strategy is marine isopods that possess three distinct tactics, differ genetically, and have equal fitness values, thus forming an evolutionarily stable strategy (reviewed in Shuster and Wade 2003). A mixed strategy is characterized by a single strategy with different tactics that are stochastically assigned among genetically identical individuals and have unequal average fitness values; these strategies are thought to be rare in nature. Finally, the conditional strategy is characterized by genetic monomorphism and unequal average fitness values among morphs. One well-known example of the conditional strategy is horned beetles in which larger larvae develop into beetles with large horns, whereas smaller larvae develop into beetles with small horns (Emlen 2000).

However, within each of these three broad classes of intraspecific polymorphism, there is substantial variability (West-Eberhard 2003). Here we focus on one particular kind of intraspecific polymorphism (labeled "age-specific forced polymorphism") that falls within the broader classification of a conditional strategy but has been considered in detail by relatively few authors (but see Moore and Thompson 1991; Brockmann and Penn 1992; Moore 1993; Brockmann 2001; see also Rhen and Crews 2002, where this issue is reviewed from a neural and hormonal perspective). Our definition poses several conditions. By "age-specific" we mean that the morphs necessarily occur at different ages, or life stages, and that the life stages are irreversible. Further, our definition considers only sexually mature members within a given sex, thus excluding morphological and behavioral changes that occur because of

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sexual development. By "forced" we mean that the younger morph must turn into the older morph (see below for a discussion of what we mean by "turn into"). Previous authors have defined morphs in the context of discrete alternative phenotypes that do not overlap (see above references), but we use a somewhat different definition of morph for the sake of this review. By "morphs" we mean the presence of two or more statistically distinguishable phenotypes within sexually mature members of a particular sex.

Because our analyses focus on phenotypically different life stages, as opposed to phenotypically different individuals of the same age, we hereafter refer to "life-stage morphs." We also emphasize that some (but not all) of the traits discussed in this review (e.g., relative head dimensions) are quantitative, and hence, although our definition requires that life-stage morphs differ in their average phenotype, there may be variability within each of these groups (in contrast to the traditionally defined morphs, for which phenotypes are often fixed). We argue that our use of the terms "polymorphism" and "life-stage morphs" is reasonable, because one of the primary points of this review is to emphasize that morphological variation within a species need not be discrete. We exclude polymorphism based on coloration because color patterns are more likely to reflect environmental conditions (e.g., dietary availability of pigments such as carotenoids) than morphological shape. While our definition could potentially apply to either males or females, we focus here on males. Throughout this review, we assume that age and size are largely correlated within vertebrates. However, as we discuss below, more demographic data linking age and size for various species would be useful for testing this assumption.

Previous authors have already reviewed the general issue of how different age groups (e.g., subadult males, adult males) exhibit alternative behavioral tactics for acquiring matings with females (e.g., sneaking vs. territorial males). Indeed, it is not uncommon for smaller, younger males to adopt a particular mating strategy only to change that strategy once they are older and larger (reviewed in Caro and Bateson 1986; Andersson 1994). Other authors have approached the issue of ontogenetic changes from a hormonal perspective, stressing that distinct male morphs could arise either because of "organizational" structural changes early in ontogeny (e.g., male dewlap color morphs in the lizard *Urosaurus*) or by changing from one morph into another because of the influence of "activational" hormonal structural changes (Moore and Thompson 1991; Moore 1993). Thus, our definition of age-specific forced polymorphism is potentially consistent with this second process described by Moore and Thompson (1991) and Moore (1993), except that those authors were primarily interested in hormonal effects on the phenotype and behavior, whereas our definition includes both hormonal and nonhormonal selective forces. We do not contend that we are the first to discuss this phenomenon, but our goal is to consider this phenomenon in a broad ecological and evolutionary context (see also Dominey 1984). Indeed, an important point of our review is that the presence of different morphs could occur either by already described activational or organizational changes ("life-stage morph maturation"; Fig. 1; Moore and Thompson 1991; Moore 1993) or by directional selection eliminating certain members of the younger life-stage morph, hence "creating" the older life-stage morph ("life-stage morph selection"; Fig. 1). We also do not contend that we are the first to consider selection on different life stages (see Fujino and Kang 1968; Berry and Crothers 1970; Hiorns and Harrison 1970; Lowther 1977; Leamy 1978; and Arnold and Wade 1984 for examples for both discrete and quantitative traits), but we argue that we are the first to syn-

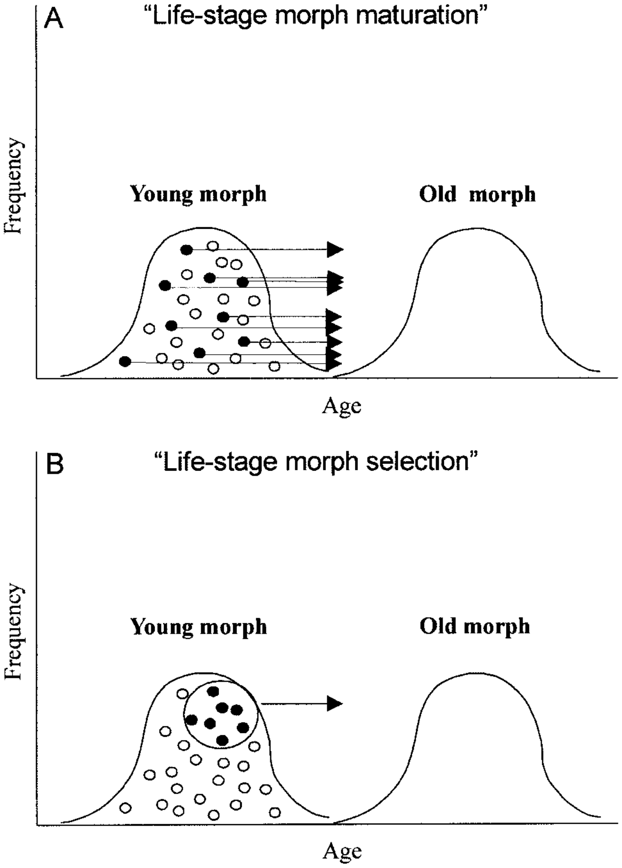

Figure 1. Heuristic depiction of the life-stage morph maturation and life-stage morph selection hypotheses potentially accounting for age-specific forced polymorphism. For both *A* and *B*, the two modes represent statistically distinct phenotypes within sexually mature males of a single vertebrate population. Note that in both cases, no males exist between these two modes. In life-stage morph maturation (*A*), all younger males have the potential to mature into older phenotypically distinct males, most likely via the influence of hormones. In life-stage morph selection (*B*), only a small, nonrandom subsample of younger males become older males, while the remainder of the younger males are eliminated by selection. Because the selection is highly nonrandom, older males therefore differ phenotypically from younger males under the life-stage morph selection hypothesis.

thesize prior studies on both life-stage morph maturation and life-stage morph selection in the broader context of male polymorphism.

A theoretical example demonstrates the difference between these two hypotheses. Consider a case of a population in which males all use a structure (e.g., a horn or antlers) in male-male combat. The structure could be used directly during fights (such as when ungulates engage in head-sparring contests), indirectly (in which males assess the relative size of the structures but rarely fight one another), or both. Within sexually mature males of this population, we observe two phenotypes: small males with small (relative to size) sexual structures and large males with large sexual structures.

We suggest that this situation could have arisen via either the life-stage morph selection or the life-stage morph maturation mechanism (Fig. 1). The life-stage morph maturation hypothesis predicts that every younger male with the smaller structure has the potential to become a larger male with the larger structure. Further, the likely mechanism behind this transformation is an activational effect of hormones that results in males developing larger structures (at a relatively fast rate) as they grow older (Moore and Thompson 1991; Moore 1993). This mechanism would then potentially result in a bimodal distribution of male phenotypes because the males all receive the activational effects of the hormones at about the same ontogenetic stage, thus allowing them to bypass any intermediate stage of structure development (Fig. 1*A*). Note that this hypothesis assumes not that every young male will survive to become an older male but simply that every younger male has the potential to develop a larger structure as it matures. Thus, the life-stage morph maturation hypothesis posits that small males will change into large males by both the process of aging and the additional process of physiological alteration (e.g., hormones). The life-stage morph selection hypothesis presents a different explanation for the pattern depicted in Figure 1. This hypothesis predicts that (1) there is variability within young males in terms of relative structure size and (2) only males with relatively large (or small) structures (relative to size) survive to become older males (Fig. 1*B*). Thus, directional selection creates phenotypic differences among life-stage morphs, creating a gap in the male frequency distribution where mortality is high.

In summary, the life-stage morph maturation hypothesis states that a bimodal distribution exists because of some activational developmental change that accelerates males past intermediate stages of structural development. By contrast, the life-stage morph selection hypothesis states that a bimodal distribution exists because the vast majority of young males are eliminated before becoming adult males and that the point of elimination is the gap present in Figure 1*B*. Thus, life-stage morph selection is most likely to occur in species in which male-male competition is extremely intense and consequently results in high male mortality. For example, young males rarely compete directly with older males in many animal species, but upon reaching a threshold size, younger males may begin to compete directly with older males (see Clutton-Brock et al. 1988). If these younger males consequently suffer high mortality rates as a result of such fights, then one should observe relatively few males at such intermediate sizes because most of them will be eliminated from the population. Thus, the life-stage morph selection hypothesis suggests that populations will be composed of a relatively small but stable pool of older, larger males and a much larger pool of younger, smaller males.

The maintenance of different life-stage morphs over ecological time by either of the two above mechanisms has not been considered previously in detail. In the case of life-stage morph selection, the two life-stage morphs should be stable temporally as long as recruitment into the smaller-male mode consistently compensates for the high mortality suffered at the gap between the two life-stage morphs and male mating success is unequal, enabling the larger males to acquire most of the valuable territories (and hence matings), forcing the younger males to attempt to cross to the other side of the gap. In cases of life-stage morph maturation, maintenance of the two life-stage morphs should be primarily dependent on the stability of the physiological mechanisms underlying the morphological changes.

Our goal was to review the literature to determine the prevalence of age-specific forced polymorphism within vertebrates. We focused on vertebrates in part to simplify our analyses and because we wanted to avoid comparing species with dramatically different reproductive patterns and social systems (e.g., vertebrates vs. invertebrates). We reviewed all articles in the journals *Proceedings of the Royal Society of London B*, *Proceedings of the National Academy of Sciences of the USA*, *Animal Behaviour*, *Behavioral Ecology and Sociobiology*, *Ethology*, *Ecology*, *Functional Ecology*, *Molecular Ecology*, *Oecologia*, and *Oikos* from the beginning of 1983 through the end of 2003 to find examples of age-specific forced polymorphism within vertebrates. We also consulted several synthetic reviews for potential examples (Andersson 1994; Shuster and Wade 2003) and conducted simple searches within the online zoological records and Cambridge Scientific Abstracts. However, as in any review, some documented cases of age-specific vertebrate polymorphism may have been missed. After presenting possible case studies of age-specific forced polymorphism, we provide an outline for researchers to consider ways in which one could explicitly test for the life-stage morph maturation and life-stage morph selection hypotheses.

Case Studies of Age-Specific Forced Polymorphism

In this section, we highlight studies that met our criteria for age-specific forced polymorphism from a review of studies published in 10 behavioral and evolutionary journals over the past 20 years. Few study systems met all of our inclusion criteria.

However, rather than deeming our criteria to be too strict, we believe that our apparent failure to detect evidence of age-specific polymorphism stems from a general lack of basic demographic information on these systems (see below and Table 1) and that therefore it is highly likely that more examples exist. In each case, we address whether the examples are consistent with the life-stage morph maturation or the life-stage morph selection hypothesis.

Broad-Headed Skinks

Male broad-headed skinks (*Eumeces laticeps*) may be a candidate for age-specific forced polymorphism because larger adult males have significantly larger heads (relative to size) than smaller adult males (Cooper and Vitt 1985, 1987). Further, these head shape differences appear correlated with differences in maximum bite force (A. Herrel and B. Moon, unpublished data). However, this head shape difference may be at least partially seasonal; larger males appear to develop enlarged heads primarily in the spring, when male-male competition is particularly intense (Cooper and Vitt 1985). Because male broad-headed skinks actively bite one another when fighting (B. Moon, personal observation), this apparent dramatic shift in head shape and bite force may also result in male mortality, as scars from fights are often substantial (Cooper and Vitt 1987). Behavioral differences are also apparent between smaller and larger males; for example, smaller males are unable to guard reproductive females (Cooper and Vitt 1987). Further, small adult males typically flee rather than fight large males, and smaller males will sneak copulations with females in the absence of large males (Cooper and Vitt 1987). Finally, larger males also tend to have a higher frequency of bite marks than smaller males, suggesting that biting as a behavioral strategy is more common in larger than in smaller males, which mirrors findings for small and large green anoles (Lailvaux et al. 2004; see "Green Anole Lizards"). Therefore, if one assumes that age and size are closely related in these lizards, as has been shown for some other reptiles, then the dimorphism appears to be age specific. However, the fact that the head shape difference is most apparent at particular seasons suggests that head shape variation among males may be influenced by hormones, and therefore one cannot definitely invoke either life-stage morph maturation or life-stage morph selection in this case.

Primates

Several primate species appear to exhibit age-specific forced polymorphism, such as the presence of flanges, or enlarged flaps of skin on the cheeks, among males of various sizes. However, basic natural history information is lacking for many species, and hence we discuss two potential cases (orangutans *Pongo pygmaeus* and mandrills *Mandrillus sphinx*).

A potential case of socially mediated expression of male sexual ornamentation occurs in semi-free-ranging mandrills, *Mandrillus sphinx* (Wickings et al. 1993; Setchell and Dixson 2001, 2003; Setchell 2003). As in orangutans, subordinate male mandrills are also known to sneak matings, because larger, flanged males are usually antagonistic toward other males (Wickings et al. 1993; Utami et al. 2002). In contrast to orangutans, however, development of secondary sexual characters in mandrills appears to be continuous and subject to a great deal of individual variation, such that there appears to be no discrete threshold between young and old males (Setchell and Dixson 2001). However, younger subordinate mandrill males have lower testosterone levels, show less development of male ornaments, and were less group associated than alpha males, suggesting that expression of ornaments is associated with age and hence rank status. Overall, based on the documented hormonal differences between males of various sizes, mandrills and orangutans appear to be strong candidates for the life-stage morph maturation

Table 1: A summary of the reviewed studies of age-specific force polymorphism

Species	Irreversible Life-Stage Difference?	Phenotypic Difference	MS or MM[a]
Green anoles (*Anolis carolinensis*)	Yes	Head shape	Likely MS
Broad-headed skinks (*Eumeces laticeps*)	Yes	Head shape	?
Orangutans (*Pongo pygmaeus*)	Yes	Cheek flanges	Likely MM
Atlantic salmon (*Salmo salar*)	Yes	Jaw, scale, fins	Likely MM
Bighorn and Soay sheep	Yes	Horns	?
Elephant seals (*Mirounga angustirostris*)	Yes	Trunk-nose	Likely MM

Note. For each species, we assess whether they met our criteria of (*a*) irreversible life-stage differences among sexually mature males and (*b*) phenotypic differences among life stages. We also note whether the observed polymorphism is more likely to have occurred via the life-stage morph selection (MS) or life-stage morph maturation (MM) mechanisms. We did not include frogs in this table because of the lack of data showing a phenotypic difference among alternative mating strategies.

[a] ? = unclear.

process, although the developmental switch point in these cases may be determined by the interaction between age/size and social status, as opposed to solely age.

Within orangutans, some (typically larger) males possess enlarged (flanged) cheeks and a throat sac that aids in the production of loud advertising calls (MacKinnon 1974; Galdikas 1985*b*), whereas other (typically smaller) sexually mature males do not possess such features. The male calls produced from the throat sac are thought to be directed primarily toward other males, as opposed to females (Mitani 1985*b*). A marked bimaturism exists among adult orangutan males, who vary widely in the age at which these sexual characters develop; in some males, the appearance of these characters may be delayed until the age of 30 (Utami et al. 2002). Nonetheless, unflanged adult males are fertile and sexually active and have been shown via microsatellite analyses to father approximately half the offspring sampled in a Sumatran orangutan population (Utami et al. 2002), although this last finding is based on a small sample size ($N = 11$) and should be interpreted cautiously.

Previous studies have also observed behavioral differences between young and old orangutan males; the larger, flanged males' tactic is that of consort/combat, while unflanged males use a combination of sneaking and sexual coercion (Galdikas 1985*a*; Mitani 1985*a*; Fox 2002). Utami et al. (2002) also suggest that the flanged males follow a sit-and-wait strategy that relies on female choice to gain matings, while unflanged males actively search out females. Maggioncalda et al. (1999) further suggest that the development of secondary sexual characters is dependent on social context in orangutans; young males may monitor the proximity and density of adult males via male calls and arrest secondary sexual development if male density is high, so as to avoid combat with flanged males. Despite this work, the "arrested-development" effect has yet to be demonstrated in orangutans in nature. In a study of captive orangutans, Maggioncalda et al. (1999) show that urinary levels of testosterone and growth hormones are higher in flanged than in unflanged males, although they also state that unflanged and flanged males may not always differ in age. Therefore, whereas the general notion of age-specific forced polymorphism is supported within orangutans, and the hormonal difference is suggestive of the life-stage morph maturation hypothesis, the lack of demographic information relating the presence of flanges to age makes it difficult to eliminate the life-stage morph selection hypothesis.

Atlantic Salmon

Fish species exhibit a bewildering array of alternative mating strategies, ranging from simple sneaker/guarder males (Taborsky 1994) to sequential hermaphroditism (Cardwell and Liley 1991). For many fish species, whether male phenotypes are genetically dependent or determined by an ontogenetic switch is unclear (Martin and Taborsky 1997). One exception to this generalization is the Atlantic salmon (*Salmo salar*). In the iteroparous *S. salar*, as well as the semelparous Pacific salmon (*Oncorhyncus* spp.), precociously mature males (parr) sneak fertilizations by darting into spawnings, whereas larger and older hooknoses fight for mating opportunities. The hooknose structure, or kype, is a result of drastic skeletal alterations in male salmon (Tchernavin 1938; Witten and Hall 2003) and is used as a weapon in male fights (Darwin 1871; Jones 1959). Other morphological changes are also associated with hooknoses, including thickening of the skin and embedding of scales within it (Fleming 1996), expression of mottled red coloration, and enlargement of the adipose fin (Naesje et al. 1988; Järvi 1990). In contrast to anadromous hooknoses, precocious parr show no development of secondary sexual characters but do differ from immature parr in both color and body form (Rowe and Thorpe 1990). In Pacific salmon species, the two strategies are necessarily fixed because males die after breeding, but in *S. salar*, precocious parr can mature into larger hooknoses (Moore 1993; Fleming 1998). An additional selective pressure is overfishing, which results in a deficit of anadromous adults and a disproportionate frequency of precocious parr (see Soay sheep example below). Thus, while the evolution and maintenance of alternative male strategies in Atlantic salmon are poorly known (Fleming 1998), the available information appears consistent with the life-stage morph maturation hypothesis.

Frogs

Many frog and toad species contain two plastic alternative male strategies. Large males are frequently brightly colored and call to attract mates, while smaller, less brightly colored males do not call but attempt to intercept females moving toward calling males (e.g., Howard 1978; Loman and Madsen 1986; Perrill et al. 1987). However, whether frogs that employ these two alternative strategies also differ morphologically is unclear. For example, previous researchers have suggested that larger males should have relatively longer arms, compared with smaller males, for grasping females, as males that can hold on to females tightly would be expected to resist displacements from competing males (e.g., Howard and Kluge 1985; Lee 1986). However, attempts to test this idea in bullfrogs have yielded equivocal results, because researchers have compared, for example, the arm lengths of adult males to those of similarly sized females rather than examining the allometry of arm length over an ontogenetic series (Howard 1988). Finally, no studies have convincingly shown that larger adult males are always older than smaller adult males (see Halliday and Verrell 1988). Therefore, while this example is not a documented example of age-specific forced polymorphism, we mention it as a promising candidate for further study. Obviously, more data are needed as well to invoke either life-stage morph maturation or life-stage morph selection.

Bighorn and Soay Sheep

Bighorn sheep males (*Ovis canadensis*) display three distinct mating tactics (Hogg 1984, 1987; Hogg and Forbes 1997). Large, mature "tending" rams defend an individual estrus ewe from other rams. "Coursing" rams attempt to sneak matings from guarded ewes, and "blocking" rams attempt to forcibly isolate ewes from the tending area until they become receptive. Coursing and blocking are the primary tactics used by younger, subordinate rams. Hogg and Forbes (1997) suggest that agility, endurance, and speed are likely to be important for successful coursing, whereas large body size and massive horns are important for tending rams. Indeed, Coltman et al. (2002) found a complex, nonlinear relationship between mating success, body size, and horn size, with horn size being relatively the most important trait for mating success only among the oldest rams (i.e., rams more than about 6 yr old). Furthermore, Festa-Bianchet et al. (2004) showed that young rams appear to allocate more resources to body than to horn growth where possible. Since approximately 75% of asymptotic horn growth occurs within the first 4 yr of life (Jorgenson et al. 1998), rams with short horns by the age of 4 yr remain small-horned over the rest of their lifetimes. Interestingly, it appears that these short-horned rams may currently have a selective advantage over long-horned rams of the same age, because young rams with fast-growing horns are likely to be shot before 6 yr of age by trophy hunters (Coltman et al. 2003; Festa-Bianchet et al. 2004). Thus, coursing rams with small horns are favored when young, but above the 6–7-yr threshold, tending rams with larger horns have greater reproductive success. The available data therefore suggest the possibility of life-stage morph selection for bighorn sheep but with a unique twist; the primary selective pressure contributing to the male dimorphism is hunting by humans, an interesting case of "unnatural" selection.

The closely related Soay sheep (*Ovis aries*) may also be a case of age-specific forced polymorphism. In this species, males exhibit two types of horns, scurred (small, apparently vestigial horns) and normal, fully developed horns, although it is not clear that this morphological difference is correlated with age. For example, these different horn phenotypes may be influenced by different sets of genes, as opposed to being discrete stages along an ontogenetic series (Ibsen 1944; Clutton-Brock et al. 1997). Male Soay sheep display marked precocial sexual maturity and begin rutting at the age of 7 mo, when they are only one-third of their adult body weight (Grubb 1974). As in bighorn sheep and other ungulates, small males may gain little from competing directly with larger males (Clutton-Brock et al. 1988), and so the probability of mating successfully increases with both body size and horn size in Soays (Preston et al. 2003). Stevenson and Bancroft (1995) also show that the survival cost to early reproduction in male Soays is high but that young males also exhibit unexpected mating success, gaining up to 15% of the matings. However, it is unclear whether juvenile males are truly adopting different behavioral tactics in this species, because success in juvenile mating appears to be maintained by periodic demographic fluctuations resulting in female-biased sex ratios within populations (Stevenson and Bancroft 1995). Therefore, while these data are suggestive of age-specific forced polymorphism within Soay sheep, more data on whether the horn dimorphism is correlated with age are needed.

Elephant Seals

Elephant seals (*Mirounga angustirostris*) exhibit two male phenotypes that appear correlated with age: very large males possess an enlarged trunk-nose, which is used to roar and hence defend groups of females, whereas younger yet still sexually mature males do not possess this trunk-nose. Correlated with this phenotypic difference is a dramatic difference in mating success; as few as five out of 180 males are typically responsible for 48%–92% of the matings observed with up to 420 females during a breeding season (Le Boeuf and Reiter 1988), and larger males typically gain most of the matings. Whereas large males will actively defend clusters of females, young males will attempt to sneak copulations with females (Le Boeuf 1974). This situation is similar to that presented above for orangutans, in which older males possess a distinct phenotypic structure that younger males do not. However, an unresolved issue is the ontogeny of the trunk-nose. Does this morphological feature appear suddenly at a certain life stage, or does it grow gradually? If the former, this would suggest that the presence of the trunk-nose is most profitably explained by the life-stage morph maturation hypothesis, in which all younger males would mature into larger males if they survived. Unlike the case for orangutans, no data are available on hormone levels in younger and older males, leaving open the possibility of life-stage morph selection.

Green Anole Lizards

Recent work (Lailvaux et al. 2004) provides some evidence for age-specific forced polymorphism in the green anole lizard (*Anolis carolinensis*). Lailvaux et al. (2004) examined a large ($N = 403$) sample of juveniles, adult females, and adult males from a natural population and found two phenotypes among sexually mature males (i.e., >48-mm snout-vent length). Larger ("heavyweight") males tended to have relatively much wider and deeper heads and more powerful bite forces, compared to smaller ("lightweight") males. Thus, as noted in the "Introduction," these life-stage morphs differ in quantitative, not discrete, morphological characteristics, which is consistent with our definition of age-specific forced polymorphism. Further, Lailvaux et al. (2004) also provide evidence for different fighting strategies that have arisen as a consequence of this ontogenetic change in performance, with the heavyweight males relying on bite performance to win staged laboratory male-male contests and lightweight males relying on jumping performance. Therefore, the ontogenetic shift in relative head shape, and consequently bite force, within green anole males has apparently resulted in behavioral shifts as well. Given the general association between size and age in reptiles (Halliday and Verrell 1988), heavyweight males are likely older than lightweight males (Lailvaux et al. 2004).

While not definitive, several lines of evidence suggest that life-stage morph selection is a more likely alternative for explaining this dimorphism. First, unlike the situation with discrete presence/absence of morphological characters (e.g., flanges in orangutans, trunk-noses in elephant seals), quantitative ontogenetic shifts in head shape after sexual maturity seem more likely to have arisen as a consequence of life-stage morph selection. Second, field studies show that green anole males compete intensely with one another to gain access to territories, often resulting in males becoming extremely weakened or severely injured by the end of the spring breeding season (Jenssen et al. 2001). Indeed, Lailvaux et al. (2004) frequently observed severe scars on adult males, many of which appear to have arisen via bite wounds from male-male fights. Therefore, a key ingredient of life-stage morph selection, namely, intense male-male competition, is present within green anoles. Third, the approximate 2 : 1 ratio of lightweight : heavyweight males (Lailvaux et al. 2004) suggests that relatively few lightweights survive to become heavyweights, also fulfilling a key component of the life-stage morph selection hypothesis. Finally, detailed behavioral studies with green anoles by T. Jenssen and colleagues has documented marked differences in mating strategies between the two anole male morphs (Orrel and Jenssen 2003; T. Jenssen, unpublished data). Their work shows that heavyweight males are highly territorial and acquire most of the matings from resident females within that male's territory. By contrast, lightweight males rarely compete directly with these large males for preferred territories but gain some matings by using a sneaking strategy in which they mimic female display patterns to avoid confrontation with the resident larger male (Orrel and Jenssen 2003; T. Jenssen, personal communication). As lightweight males become larger, they are also more likely to engage in confrontations with resident heavyweight males (T. Jenssen, personal communication), and these confrontations could be a significant factor in male mortality, because of the large amount of energy expended by males during the breeding season. Despite this evidence, more long-term demographic and laboratory data are needed to definitively show that life-stage morph selection is responsible for the observed male polymorphism.

Synthesis

In this article, we have examined cases of age-specific forced polymorphism that are analogous to the plastic alternative reproductive strategies described by Moore and Thompson (1991) and Moore (1993). Several key findings emerge from our review. First, we were able to clearly detect only a few cases of age-specific forced polymorphism. One possible reason is that this phenomenon is rare in nature. However, we examined many studies that might have fit our criteria but lacked basic information (e.g., age or size of morphs, whether the morphs differ morphologically), making inclusion into our review impossible. A recurring problem for all of the studies reviewed here is determination of the age of morphs, and while some of the studies reviewed here provide good data on the ages of animals, others do not, and hence this assumption requires more testing.

Second, even for the documented examples in Table 1, we were unable to definitively discern either life-stage morph selection or life-stage morph maturation, although for some systems (e.g., orangutans, Atlantic salmon), some evidence suggested that one hypothesis (e.g., life-stage morph maturation) was more likely than the other. Indeed, a central point of our review is that researchers interested in male polymorphism should consider designing experiments and field studies that will explicitly test for these hypotheses. First, it is important to note that simple mark-recapture data alone would not resolve these hypotheses; additional data on either the presence/absence or the shape of the morphological structure in question (e.g., head shape in green anole, flanges and throat sacs in orangutans) for marked individuals would also be needed. To test for life-stage morph selection, we also suggest that researchers should examine for evidence of high mortality at particular points in ontogeny. Second, studies of the growth of such morphological structures might reveal whether these structures change gradually with age or appear suddenly at a particular life stage. Third, hormone manipulations might shed light on whether the structure increases or decreases based on the presence of a particular hormone, which would support the life-stage morph maturation hypothesis. Fourth, because the life-stage morph selection hypothesis predicts that variation in male morphology is generated by natural selection, then one might be able to comparatively test these hypotheses by raising juveniles in the laboratory from birth through death, thus preventing selection from occurring. If the observed polymorphism occurs in nature but not in the laboratory over the same time period, then one might conclude that the life-stage morph selection hypothesis was the more likely explanation for the presence of distinct morphs. Naturally, such laboratory rearing studies might not be feasible for some species (e.g., elephant seals) and also could introduce some artifacts that may not be present in natural systems, so such laboratory results would have to be interpreted with caution. For example, laboratory rearing experiments would not eliminate the possibility that morphological changes are caused by social influences.

Overall, we suggest that long-term mark-recapture studies and laboratory rearing studies could be a powerful combination for resolving these two hypotheses. Accordingly, we suggest that future studies in the general area of male polymorphism consider gathering long-term mark-recapture data for understanding the origin of the morphs, and we echo Brockmann's (2001) call for more integrative studies of alternative phenotypes. Indeed, a central point of this review is the importance of integrating life-history theory for understanding sexual selection.

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