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PERSPECTIVES IN ORNITHOLOGY

PUTTING SEXUAL TRAITS INTO THE CONTEXT OF AN ORGANISM: A LIFE-HISTORY PERSPECTIVE IN STUDIES OF SEXUAL SELECTION

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BECAUSE SEXUAL TRAITS are often so striking, even bizarre, and seemingly different from other traits, researchers commonly study those traits in isolation from the rest of an organism, drawing evolutionary conclusions from the relation between the expression of a sexual trait and current reproductive success. However, because adaptation results from lifetime performance of an entire organism, it is not generally warranted to study the evolution of sexual displays in isolation from the performance of the entire organism and from the organism's interactions with its ecological and social environment.

Moreover, it is often assumed that the evolution of elaborate sexual displays is favored by mate preferences for further exaggeration. That is because the costs associated with the production and maintenance of a more exaggerated ornament are expected to facilitate the condition-dependence of ornament expression (Zahavi 1975, Andersson 1982, Grafen 1990). In turn, females mating with the most ornamented males are assumed to choose the best adapted mates that should sire the best adapted offspring (Andersson 1986, Pomiankowski 1988, Iwasa et al. 1991) and provide females with more phenotypic benefits (such as help with raising offspring; Hoelzer 1989, Price et al. 1993). However, recent empirical studies suggest that the coevolution of male sexual displays and female preference is not as straightforward as described above, because both the expression of sexual displays and the preference for these displays are often specific to the social and ecological environment of breeding.

More generally, the view of sexual trait expression and preference as uniform and open-ended characters that can be studied in isolation from the rest of an organism have left a number of unresolved questions. First, whereas a positive relationship is expected between sexual trait elaboration and direct benefits, empirical studies often document highly variable relationships both between and within populations (e.g. positive association, Hill 1991; negative association, Studd and Robertson 1985; no association, Sundberg and Larsson 1994). Second, abundant phenotypic and genetic variance in expression of sexual traits (Møller and Alatalo 1999) is difficult to reconcile with the expectation that consistently strong and long-term directional selection for a greater expression of those traits should remove that variation. Third, it is unclear how sexual displays that reliably indicate local adaptation (e.g. diet-dependent ornamentation) can nevertheless persist across a wide range of environments. Finally, the assumption of consistent and open-ended mate preference is difficult to reconcile with the findings that the benefits ac-

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quired from mate choice are often environment-specific and even individual-specific (Widemo and Sæther 1999, Tregenza and Wedell 2000, Qvarnström 2001).

Those questions emphasize the need for a better conceptual framework in which to address the evolution of sexual displays and preferences. The focus of recent studies has been the explicit integration of an organismal perspective into sexual selection studies. The central thesis of this approach, and the focus of this article, is that the investment in trait expression and the investment in mate choice are parts of the reproductive investment of an entire organism and thus are subject to life history trade-offs within an organism as well as the effects of social and ecological environment in which breeding occurs. Here we review recent avian studies that demonstrate the importance of an organismal perspective on the expression of sexual displays and preferences.

STATE- AND CONTEXT-DEPENDENT INVESTMENT IN SEXUAL DISPLAYS

Investment in sexual ornaments depends on the investment in other costly traits and behaviors (Andersson 1982, Partridge and Endler 1987, Höglund and Sheldon 1998, Badyaev and Hill 1999). Life-history trade-offs therefore impose constraints on the evolution of exaggerated ornaments and vice versa, and those trade-offs can manifest themselves both within and across reproductive attempts (Gustafsson et al. 1995, Badyaev 1997, Badyaev and Ghalambor 2001).

Within a current reproductive attempt, trade-offs may occur between investment in a sexual trait and investment in paternal behaviors (Qvarnström 1997, Griffith et al. 1999a, Griffith 2000, Qvarnström et al. 2000a, Sanz 2001). For example, selection should not favor the costs of ornament production or maintenance that would reduce parental care (Fitzpatrick et al. 1995, Johnstone 1995a, Martin and Badyaev 1996). Across reproductive attempts, the relative investment in sexual ornamentation, parental care, and survival varies with an individual's age and breeding history (Gustafsson et al. 1995, Kokko 1998, Sheldon 2000a). Younger individuals with greater future breeding prospects or individuals paired with lower quality mates may invest less parental care into the current reproductive attempt than is indicated by their sexual trait, whereas old males may invest more in level of ornamentation as compared to young males (Kokko 1998). Similarly, some males may invest relatively more effort in their competitive ability at the expense of parental care (Qvarnström 1997, Qvarnström and Forsgren 1998).

Thus, the current expression of a sexual ornament or display represents a solution to a trade-off between the competing demands of different aspects of reproduction and survival. However, the ways by which those trade-offs are solved vary because of individual differences in residual reproductive value, and because of variation in the social and ecological environment of breeding. Kokko (1998) modeled the optimal allocation of resources between the level of ornamentation, parental care, and future survival in males and found that males in good condition achieve greater fitness by investing resources into sexual display rather than into parental care when mating opportunities are frequent. When mating opportunities are scarce, males in good condition maximize their fitness by investing resources in both display and care. Hence, a positive relation between male ornamentation and parental care is expected when mating opportunities are rare (e.g. in monogamous mating systems) but not when mating opportunities are abundant (e.g. in polygynous mating systems). That may provide a possible explanation for highly variable relationships between ornamentation and care often found by empirical studies (see above).

To investigate the underlying selective forces behind the evolution of sexual displays, a useful empirical approach is to examine within-species variation. Carotenoid-based sexual ornamentation of the House Finch (*Carpodacus mexicanus*) is a condition-dependent sexual trait, such that males in better health and physiological condition have greater (redder) ornamentation (Hill 2000). Interestingly, the relation between the expression of that sexual trait and male parental care differs among populations. In two eastern North America populations, males with redder plumage pair with females that nest earlier and feed their incubating mates more than do yellow males (Hill 1991, Hill et al. 1999), suggesting that in those populations, a greater elaboration of condition-dependent sexual trait reliably and consistently indicates greater investment in male parental care. Interestingly, those observations differ substantially from what is observed in a Montana population of House Finches, where males use distinct reproductive tactics depending on the elaboration of their sexual ornamentation (Badyaev and Hill 2002). Males with red pigmentation pair with females that nest earlier, but those males provision incubating females and nestlings little. In contrast, males with yellow coloration pair with females that nest later, but those males feed female and nestlings more. Thus, there are pronounced differences between a single strategy of allocation into sexual display versus parental care by males in the eastern populations and the multiple strategies of males in the Montana population. Those differences however can be reconciled if the ''switchpoints'' between different reproductive tactics (combinations of sexual displays and parental behaviors) are influenced by ecological and demographic parameters, such as by highly distinct patterns of the expression of ornamentation (wide range of expression in Montana, narrow range in the eastern United States), and by the patterns of female learning and experience (demographic differences between the eastern and the Montana populations).

Variation in male reproductive tactics have also been found in a population of Collared Flycatchers (*Ficedula albicollis*), breeding on the Swedish island of Gotland in the Baltic. Among males arriving early to the breeding grounds, males with large forehead patches (i.e. highly ornamented) have a greater premating effort and are in poorer condition at the time of feeding offspring as compared to less ornamented males (Qvarnström 1999a). Consequently, early breeding females paired to large-patched males on average produce fewer fledged offspring as compared to females paired to small-patched males (Qvarnström et al. 2000a). From the male point of view, it is probably adaptive to invest more in competition over mating early in the season when there are more unoccupied breeding sites (facilitating polyterritoriality) and more females remain unfertilized. Because female Collared Flycatchers only lay one clutch per season, the proportion of fertilizable females declines as the proportion of incubating females increase. In addition, males experience an advantage in sperm competition when cuckolding other males breeding later than themselves (Sheldon and Ellegren 1999). Among males arriving late, large-patched males do not have a greater premating effort (Qvarnström 1999a) and there is a positive relationship between male patch size and female reproductive success (Qvarnström et al. 2000a).

Individual differences in acquisition and allocation of resources may have a genetic basis and thus per se be a subject of female choice (Møller and Thornhill 1998, Møller and Jennions 2001). Because the optimal allocation differs between the ecological and social environments in which breeding occurs, so will the genetic benefits of mate choice (Qvarnström 2001). For example, a male genotype that allocates a proportionally large amount of resources to sexual display at the expense of survival (Brooks 2000) may suffer a net fitness cost due to severely lowered survival of male offspring under poor environmental conditions (e.g. Reznick et al. 2000). If the male allocation scheme is reflected in the development of male's sexual trait and is heritable, females should modify their preference of male display to a level most suited to the environment of breeding. Thus, whereas the expression of male display may be the ultimate target of selection for higher fitness, the proximate target is individual variation in the ''rules'' that govern acquisition and allocation of resources to the components of reproduction.

Those examples illustrate that the correspondence between male genotype and male mating phenotype (a combination of sexual and parental behaviors and sexual ornamentation) often is state- and context-dependent. Thus, it is an oversimplification to assume that the elaboration of a sexual trait should always be positively associated with all components of fitness or even with overall fitness. Instead, this association is best understood by examining the relative investment of resources between mating competition and other costly traits and behaviors. Overall, selection may favor plasticity in components of reproductive investment and favor individuals that adopt the reproductive tactic that allows them to achieve the highest fitness under variable conditions of breeding (Gross 1996, Cunningham and Birkhead 1998). In turn, the decision to adopt a particular suite of reproductive behaviors can be phenotypically indicated by elaboration of the sexual trait (Qvarnström 1999a).

STATE- AND CONTEXT-DEPENDENT MATE CHOICE

A female's investment in mate selection can be viewed (just as male's investment in a display trait) as a state and context-dependent reproductive decision (Jennions and Petrie 1997, Hall et al. 2000, Kokko and Monaghan 2001). Moreover, when benefits from mate choice are context-dependent, selection should favor context-dependent mate preferences (Wagner 1998, Widemo and Sæther 1999, Qvarnström 2001).

However, context-dependence of the benefits obtained from mate choice presents a problem for the evolution of adaptive mate choice. A solution to that problem can include several strategies. First, females can select directly on a male's performance, including in nonbreeding settings, instead of (or in addition to) preference for the expression of a sexual display. Such mate selection may be especially common in environments where females obtain only direct (phenotypic) benefits from mating. Mate choice can be based on the acquisition of resources through male competition (i.e. selection on male's acquisition of status in winter flocks, or on male's acquisition of the cental position on a lek; see also Kokko et al. 1999, Qvarnström et al. 2000b), on previous familiarity with the partner's breeding performance (Wachtmeister 2001), or on direct observation of male parental care (Wagner 1997). Second, females can modify their mate preferences as they learn to discriminate better between different expressions of display and different reproductive strategies. Experience-related variation in female preference often determines the fitness consequences and relative frequency of alternative reproductive tactics of males (Alonzo and Warner 2000). For example, in the Montana House Finch population, females breeding for the first time compensate for low nestling provisioning of their red mates, whereas more experienced females avoid pairing with red males, preferring to pair with yellow and intermediate males instead. Correspondingly, among males breeding for the first time, redder males achieve the highest fecundity, whereas among older males, redder males have the lowest fecundity. Overall, among older females, previous experience with male's breeding performance was more important for pairing decisions than was the elaboration of the male sexual trait (Badyaev and Hill 2002).

Third, females may simply prefer the expression of a display trait that indicates the most common or most productive natal environment or the most common allocation rule. Fourth, females can base their preference on their own phenotype or genotype (self-referential choice). Strong support for a self-referential mechanism of mate choice comes from within-species studies of genetic compatibility, where it is found that a particular combination of individual male and female genotypes (e.g. in MHC complex; Grahn 2000) produces the highest fitness (Tregenza and Wedell 2000). However, whether the higher fitness of offspring from self-referential mating results from of heretozygosity *per se* (enabled by self-referential mating; Bensch et al. 1994, Brown 1998) or is due to genetic compatibility (von Schantz et al. 1996, Johnsen et al. 2000) is not currently known in birds. Moreover, female choice of genetically compatible mates may occur at the level of sperm selection, in the absence of assortative phenotypic mating (Kempenaers et al. 1999, Johnsen et al. 2000). Alternatively, phenotype matching is known in avian species where the expression of homozygosity is genetically linked to morphological traits used in mate choice (e.g. Houtman and Falls 1994, Krüger et al. 2001). Fifth, mate choice may be guided by sexual imprinting, when birds show preference for the phenotype of relatives or locally born individuals. Originally proposed as an explanation of preference for local song dialects, sexual imprinting gained much support in recent studies of other sexual displays and sexual behaviors (Irwin and Price 1999), including imprinted preference for novel sexual traits (Witte and Curio 1999) and preference for maladaptive sexual traits (Krüger et al. 2001). Sexual imprinting can enable adaptive female choice of a context-dependent male sexual trait, because it provides a common environmental link between trait preference and trait expression, that is, provides a self-referential environmental matching. For example, preference for genetically compatible mates can be formed as a result of imprinting (Tregenza and Wedell 2000).

Mechanisms enabling adaptive plasticity in female choice are likely to complement each other and their contribution may vary throughout a female's lifespan. For example, an initially imprinted preference for male sexual display can serve as a threshold for further discrimination among males. When a female is exposed to more breeding partners and is able to better discriminate among them (Weary et al. 1993), individual experience and the direct choice of male reproductive performance may play a greater role than the initial sexual imprinting (Nagle and Kreutzer 1997).

The relative importance of direct and indirect benefits of female preference for a male sexual trait (Møller and Thornhill 1998) and the cost of mate choice (Jennions and Petrie 1997) can change with a female's physiological condition and experience. For example, if a male sexual trait consistently indicates low direct benefits but high individual condition and if that allocation scheme is heritable, then females in good condition may prefer to mate with more ornamented males because the genetic benefits they would obtain would exceed the costs of reduced parental care, for which they are able to compensate (Qvarnström and Forsgren 1998, Gowaty 1999, Forstmeier et al. 2001). Thus, the relationship between male sexual display, female preference, and reproductive success can only be understood by considering the state of an individual and the context of breeding. That is well illustrated by differences between population-wide and individual female preferences (Wagner 1998), by differences in within-pair and extra-pair mate choice (Johnstone et al. 1996), as well as by variation in reproductive investment due to discrepancies in the quality of mating partners (Weatherhead and Robertson 1979, Burley 1988, de Lope and Møller 1993, Petrie and Williams 1994, Lessels 1999, Cunningham and Russell 2000, Sheldon 2000a). In the latter case, changes in reproductive investment in relation to quality of the mating partner can be viewed as a particular case of context-dependent reproductive investment. In Collared Flycatchers, females adjust both mate preference and reproductive investment to the seasonal variation in male reproductive tactics. Large-patched males are only preferred as a social mate among late-breeding females. In addition, females adjust the size of their clutch in relation to the expected quality of the breeding situation as predicted both by male patch size and timing of breeding (Qvarnström et al. 2000b). A large forehead patch on the male only seems to stimulate the female to lay large clutches when breeding late (i.e. when they expect a relatively good breeding situation). In this case, ''investment matching by the two partners'' might be a better term than ''differential investment by the female.''

IMPLICATIONS FOR THE COEVOLUTION OF PREFERENCES AND PREFERRED TRAITS

The evolution of reproductive tactics of males and females is tightly linked through a combination of common fitness interests and conflicts. The overall challenge that both mating partners face is to match optimally the investment in sexual display or in mate selection with the social and ecological setting in which breeding occurs. Depending on the overlap in fitness consequences of a breeding attempt between the mating partners, the optimal matching of male and female interests is likely to involve a combination of collaboration and manipulation. Both of those strategies require extensive communication between mating partners and thus facilitate the evolution of appropriate sexual displays and behaviors. The challenge to future studies is to investigate the role of sexual displays in collaborative or manipulative communications between mating partners as well as, on a more proximate level, the extent to which sexual displays indicate variation in acquisition versus allocation of resources to breeding.

Overall, female preference should favor sexual displays that are closely linked to individual condition (Kodric-Brown and Brown 1984). However, different aspects of male condition are likely to be important to different females and in different environments (Wedekind 1992, Schluter and Price 1993, Zuk and Johnsen 1998, Day 2000). Moreover, the precision with which male sexual displays indicate physiological condition may change with age (Hansen and Price 1995, Kokko 1997). Those two factors should favor the evolution of composite sexual traits whose components are linked to different organismal processes. Variable dependence on different aspects of condition in combination with variable female preference for individual components of a sexual trait should result in the evolution of composite sexual traits whose components reliably reflect condition across a wide array of breeding environments (Badyaev and Hill 1999, Badyaev et al. 2001). For example, different components of carotenoid-based sexual ornamentation in the House Finch (ornament area, color hue, color consistency) have different dependencies on environmental variation and individual condition (Hill 1992). Correspondingly, distinct components are favored by different females and in different environments (Badyaev et al. 2001). Moreover, a composite sexual trait can enable more efficient assortative and self-referential mating (Wedekind 1992). That is especially the case for composite sexual traits that take a long time to develop and thus are more likely to ‘‘summarize’’ individual history and integrate more components of an individual’s ‘‘average’’ condition across its lifetime (Kokko 1997). For example, among multiple sexual traits, the traits with different temporal integration with condition (such as long-growing spurs vs. plumage traits in Wild Turkeys [*Meleagris gallopavo*], Badyaev et al. 1998; or behavioral vs. plumage displays in the Dark-eyed Juncos [*Junco hyemalis*], J. A. Hill et al. 1999) can provide different information to females thus facilitating the most optimal context- and state-dependent mate choice (Møller and Pomiankowski 1993, Johnstone 1995b). Studies of the ontogeny of sexual ornaments provide much needed insight into understanding of the evolution of context-dependent expression in sexual displays (Griffith et al. 1999b, Qvarnström 1999b, Sheldon 2000b).

One promising approach to the study of mating phenotypes is the investigation of the proximate mechanisms that govern different aspects of mating effort (Moore 1991; Ketterson and Nolan 1992, 1999). For example, high parental care of male house finches is proximately linked to both elevated levels of prolactin (R. A. Duckworth et al. unpubl. manuscript), and a decreased level of testosterone (Stoehr and Hill 2000). Production of both hormones depends on physiological condition and health (Duckworth et al. 2001, R. A. Duckworth et al. unpubl. manuscript). Interestingly, in the Montana population, males with more elaborate traits invest less in prolactin production and correspondingly into parental care and, by avoiding costly parental care, retain higher physiological condition during breeding (R. A. Duckworth et al. unpubl. manuscript) and have greater postbreeding survival (Badyaev and Martin 2000). In this case, the common condition-dependence of prolactin and testosterone production may provide a proximate link behind the evolution of alternative reproductive tactics in different populations. More generally, the investigation of proximate mechanisms that govern the allocation of resources between sexual displays and parental behaviors is especially informative for understanding the evolution of sexual displays and mating preferences.

CONCLUSIONS

Individual plasticity in allocation to breeding in males and females should favor the evolution of context- and state-dependent reproductive tactics. On an individual level, such optimization can be mediated by context- and state-dependent expression of sexual displays and the preference for such displays. On the population level, variable reproductive tactics should result in a condition-mediated association between the expression of a sexual display (which indicates an individual’s average condition in many contexts) and the benefits that the individual can provide (which indicates allocation into reproductive effort in relation to average condition). Depending on the population variation in the contexts of breeding (e.g. demographic composition), the association between average condition and average performance can enable the evolution of general preference for a sexual trait by females. Variation in that preference therefore reflects individual optimization of mate choice. Thus, to understand the evolution of sexual traits and sexual behaviors, we need to widen our approach to the study of mating phenotypes that include integration of morphology and behavior for both sexes. Moreover, an appreciation of individual variation in reproductive behaviors is an important step in establishing the selective pressures and mechanisms underlying the operation of sexual selection.

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