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CAN BREEDING HABITAT BE SEXUALLY SELECTED?

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I propose that sexual dynamics, through mechanisms of sexual selection, can in part determine what constitutes specific breeding habitat. In this view, breeding-habitat features chosen by organisms, like certain morphological or other behavioral traits they exhibit, can be sexually selected, with the consequence that breeding habitats may not be uniquely aligned for ecological niche requirements. I distinguish sexual selection from natural selection because I mean to contrast sexual natural selection (sexual selection) from nonsexual natural selection (ecological selection). Thus, I suggest that ecological selection, acting on traits related to physical resources, and sexual selection, acting on traits related to mate choice, are potentially conflicting forces acting on breeding-habitat specificity.

It is hardly novel to contend that sexual relations influence spatial patterns, but those influences have always been believed to operate within the confines of habitat sculpted by ecological selection. Here, sexual selection defines, in part, what constitutes breeding habitat.

Certain predictions arise if sexual selection generates breeding-habitat specificity. Breeding habitat must be specific, though regional differences, including dramatic ones, are consistent with the idea. A shift in, or relaxation of, such specificity in nonbreeding situations is expected, given the flexibility in exploiting resources. Generalized traits, such as beaks equipped to exploit a variety of food sources, are predicted to prevail, because adaptive constraints from one period may compromise adaptive solutions for another. Finally, we would expect social factors to influence habitat occupancy

patterns, with spatial clustering, independent of ecological factors, likely. Although none of the foregoing is independent direct evidence that breeding-habitat specificity is a sexual trait mediated by sexual selection, collectively it supports the concept. I suggest that the idea has general applicability, but I focus primarily on migrant birds as a group, because they are especially suited for its consideration.

Breeding-habitat specificity.—Habitat specificity is believed to result from evolution of adaptations ecologically selected for the exploitation of niches found in particular habitats. Ecomorphology literature (e.g. Selander 1966, Leisler 1980, Bairlein 1980, James 1982, Polo and Carrascal 1999) both rests on and supports the premise that the morphologies of birds are suited to the niches and habitats they occupy. As a corollary, the notion that organisms should settle in habitats of high intrinsic quality is pervasive (Fretwell and Lucas 1970, Rosenzweig 1991, Ens et al. 1992, Yosef and Grubb 1994). Brown et al. (1995) argued that “hotspot” concentrations of within-species avian breeding territories, noted by many (e.g. Nice 1937, May 1949, Morse 1989, Jones and Robertson 2001), reflect the extent to which local habitats satisfy the niche requirements of particular species. Certainly, habitat features can be connected to reproductive success (Krebs 1971, Holmes et al. 1996), though fecundity thresholds are met under conditions of excessive food (Tremblay et al. 2003).

Moreover, there is no doubt that birds are habitat-specific, especially during breeding. In a classic paper, MacArthur et al. (1962) began by noting that a competent bird-watcher can “look at a habitat and correctly name the bird species that will breed there in abundance.” Numerous studies of North American breeding bird

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communities have found highly nonrandom distributions among plant alliances (Debinski and Brussard 1994, Welsh and Loughheed 1996, King et al. 2000). Paradoxically, that pattern is especially emphasized among those species whose breeding and winter habitats are most dramatically different—Neotropical migrants (Kirk and Hobson 2001).

Breeding-habitat specificity sometimes shows distinct regional variation within species, indicating adaptedness to multiple, though regionally specific, habitats. Hammond's Flycatcher (*Empidonax hammondi*), Prairie Warbler (*Dendroica discolor*), and Swainson's Warbler (*Limnothlypis swainsonii*) are examples in which distinctly different habitats are occupied on a regional basis (Nolan 1978, Lambert 1987, Brown and Dickson 1994, Willson and Comet 1996). Flack (1976) reported other instances of habitat switches in birds of the American southwest.

Reduced habitat specificity at other times.—Notwithstanding breeding-habitat specificity, most migrant species are capable of successfully occupying very different habitats. Even during breeding, there is evidence that nonbreeding habitats are used cryptically for foraging in some species (Lack 1943, Pagen et al. 2000). Other species, when no longer limited by nesting requirements, but prior to autumn departure, broaden the range of habitats exploited (Anders et al. 1998). During migration, birds are less habitat-specific (Wang and Finch 2002), which is not surprising given the variety of environments they pass through and the imperfect information they have access to en route (Shochat et al. 2002). Migrant passerines can be habitat-specific during winter (Murphy et al. 2001), but diverse habitats are frequently occupied during that season (Wunderle and Waite 1993, Latta and Faaborg 2002).

It is arguable that the increased energy demands of reproduction could select for more highly restricted breeding habitat to maximize foraging success. However, molt costs and migration also are energetically demanding, and even in the tropics, studies of foraging (Thiollay 1988, Lovette and Holmes 1995) and stress (Norris et al. 2004) in migrant passerines suggest that energy demands are not easily met during nonreproductive periods. Whether winter conditions are more limiting than breeding conditions, as collective research suggests they may be (Lack 1943, Lozano and Lemon 1998, Confer

and Larkin 1999, Katti and Price 1999, Strong and Sherry 2000, Evans et al. 2002, Tremblay et al. 2003; but see Newton 2004 for review), adaptations to breeding conditions are likely to be con-founded or at least compromised by prevailing adaptations for nonbreeding situations.

In fact, given the multitude of environments that migrants experience over the course of a year, flexibility in exploiting different habitats is a necessity. Eight of 18 passerines breeding in interior Alaska remain there for approximately three months or less, with a mere 48 days being the average for Alder Flycatchers (*E. alnorum*) (Benson and Winker 2001). Blackpoll Warblers (*D. striata*) primarily breed in stunted spruce (*Picea* sp.) taiga but winter in tropical forests of the western Amazon (Dunn and Garrett 1997). To the extent that such different habitats pose different challenges, adaptive responses must reflect compromises, with a measure of niche-averaging.

Resource exploitation within habitats is also varied.—Not only do many species cope well with highly variable environments, empirical studies of migrant species have demonstrated that resource exploitation is highly flexible, arguing for further ecological plasticity. Many studies of guilds of coexisting species have documented overlaps in exploitation of food resources, both in temperate (Wiens 1977, Paszkowski 1984, Holmes 1986, McKnight and Hepp 1998, Rotenberry and Wiens 1998, Ruth and Stanley 2002, Katzner et al. 2003) and in tropical breeding systems (Gotelli et al. 1997, MacNally 2000), especially when food is superabundant (McMartin et al. 2002). Even MacArthur's (1958) study of spruce-forest-breeding warblers indicated large overlaps in the exploitation of foraging resources by congeneric species. In addition, within-species flexibility in foraging techniques among migrants has been frequently demonstrated (Busby and Sealy 1979, Maurer and Whitmore 1981, Holmes 1994, McCaffery 1998, Chernetsov 2002).

Social factors influence where birds settle.—The conventional notion of niche suggests that organisms choose habitats on the basis of ecological factors and that fitness is expected to decline as density increases (Maynard Smith 1974, Halama and Dueser 1994, Ovadia and Abramsky 1995). Yet the evidence that individuals overwhelmingly select unsaturated habitats is lean (Stamps 1991). For instance, foraging

flocks of mixed species are commonplace in both nonbreeding temperate (Morse 1970, Gaddis 1980, Szekely et al. 1989, Dolby and Grubb 1999) and tropical (Winterbottom 1949, Greig-Smith 1978, Eguchi et al. 1993, Hutto 1994) passerine communities. Although those social factors are not sexual, such patterns indicate that the prevailing determinant of what area to occupy can be social, rather than resource-based.

Social attraction influences far more than foraging groups, however (Smith and Peacock 1990, Reed and Dobson 1993, Doligez et al. 2002). Conspecific attraction, the tendency for an individual to settle near individuals of the same species, influences settlement patterns in many breeding passerines, for example, Pied Flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1982), Least Flycatchers (*E. minimus*; Tarof and Ratcliffe 2000), House Wrens (*Troglodytes aedon*; Muller et al. 1997), Bearded Tits (*Panurus biarmicus*; Hoi and Hoi-Leitner 1997), Black-capped Chickadees (*Poecile atricapillus*; Ramsay et al. 1999), and tropical passerines (Collias and Collias 1969). Where breeding territories may be clustered because of conspecific attraction (Stamps 1988, Tarof and Ratcliffe 2004), local breeding density may not be a good predictor of habitat quality for any particular species.

Some contend that conspecific attraction results because new arrivals, in considering their own prospects, assess and rely on the reproductive success of conspecifics as a kind of "public information" (Forbes and Kaiser 1994, Danchin et al. 1998, Doligez et al. 2002), indirectly selecting for aggregations. As such, the information from such social cues is used to make ecologically advantageous habitat choices. Alternatively, aggregations may be directly selected, as when individuals seek benefits of aggregations such as shared vigilance (Kenward 1978, Popp 1988) or mating opportunities (Wagner 1993, 1998; Hoi and Hoi-Leitner 1997).

Social attraction does not always serve to promote settlement in ecologically advantageous habitats. Muller et al. (1997) concluded in their long-term House Wren study that newcomers established all-purpose territories near conspecifics in preference to isolated territories of equivalent quality, which is similar to the findings of Stamps (1988, 1991) in her studies of anole lizards (*Anolis* sp.). In reviewing the concept of indirect mate choice, Wiley and Poston

(1996) cited work on marine fish (Warner 1988) and lekking birds and mammals (Wiley 1991) in concluding that mating can occur at predetermined locations that have an arbitrary and traditional component. They argued that the advantages of avian nesting aggregations for indirect mate choice could be evolutionarily stable, even though there may be some ecological disadvantage to the location.

Although the concepts of aggregations resulting from mate choosiness (Wagner 1993, 1998; Hoi and Hoi-Leitner 1997) or of aggregations used in indirect mate choice (Wiley and Poston 1996) employ sexual selection thinking, the sexual selection acts to cluster individuals but does not act to define species-specific habitat. Habitat specificity remains an ecologically, not sexually, designed trait.

Why consider sexual selection in explaining habitat patterns?—Given the (1) prevalence of breeding-habitat specificity, (2) cryptic use of nonbreeding habitats during breeding, (3) tremendous ability to use and occupy multiple habitat types, (4) relaxed or varied habitat preferences during nonbreeding periods, (5) flexibility in resource exploitation, (6) selective pressures exerted during nonbreeding situations, (7) social attraction to other birds both in settling breeding territories and during nonbreeding foraging, and (8) clustered patterns of breeding territories, I suggest that the stereotyped breeding habitat preferences of many migrant passerines are not satisfactorily explained by recourse to ecological selection.

Consider the Kirtland's Warbler (*D. kirtlandii*), a rare passerine that exhibits several extreme traits in this regard. It has a small breeding range in central Michigan and winters in the Bahamas. According to Mayfield (1960, 1992), its rarity is primarily a consequence of its small and specialized breeding habitat—young jack pine (*Pinus banksiana*) woodlands 2–6 m high. Breeding territories are clustered, and tracts that seem marginal are sometimes occupied, whereas others that seem ideal are empty of birds. To assert that a species is adaptively restricted (*sensu* ecological selection) to such a narrow breeding habitat when it spends one-third or more of its year in Bahaman scrub and several other months in varied migration-route habitats stretches credibility.

The work of Willson and Comet (1996) in boreal passerine communities provides additional

possible examples of birds whose breeding-habitat traits are not sufficiently explained by ecological niche. They found that some breeding birds typically associated with conifers foraged primarily in deciduous foliage; in the cases of Ruby-crowned Kinglet (*Regulus calendula*) and Hermit Thrush (*Catharus guttatus*), one or two spruce trees in hardwood situations were frequently enough for territory establishment. One might suggest in such cases that one or two trees can meet a species' ecological need for conifers, especially if the adaptation is not for foraging (e.g. nest sites; Steele 1993). Yet that leaves us to wonder why such species are normally associated with substantial conifer representation when they can breed as well in deciduous habitats. Ecological release, in which the absence of competitors allows niche expansions (Cox and Ricklefs 1977), is another possible explanation; yet the boreal communities that Willson and Comet (1996) studied included numerous deciduous forest passerines.

When early students of evolution were puzzled by certain physical and behavioral traits that could not easily be explained by ecological selection, sexual selection provided an alternative and largely satisfactory framework for consideration. In considering puzzling aspects of avian breeding-habitat specificity, sexual selection may similarly be of assistance. Could elements of breeding habitat be a sexual commodity? More particularly, could preference for specific breeding habitat be a secondary sexual trait that, in proportion to its degree of manifestation by (1) the obtaining of space within it (by males) or (2) the selection of such males (by females), lends reproductive advantage to those individuals more strongly manifesting it? Even though it seems counterintuitive for an individual to select a site by choosing habitat features that do not optimize ecological opportunities, evolution has altered countless physical and behavioral traits in producing a rich variety of sexually selected systems (Andersson 1994). Provided that such sexual selection pays reproductive dividends, those traits can be neutral or even deleterious with respect to survival. So long as the sexual benefits afforded by one habitat have stronger consequences for reproductive fitness than ecological benefits afforded by alternative habitats, there is no *prima facie* reason why sexual selection should not exploit breeding habitat as a commodity in sexual relations.

The sexual selection literature is rich in empirical and theoretical studies. Several paradigms have had substantial circulation, and below I assess their applicability to the idea of sexually selected habitat. Three well-established models are direct benefits, indirect benefits, and sensory drive (Kokko et al. 2003). Sexual conflict (Trivers 1972, Parker 1979), which shifts the focus from benefits to costs, and species recognition are other paradigms for considering breeding habitat as a secondary sexual trait. For models that might generate sexually selected breeding habitat, Box 1 demonstrates the manner in which those models could work.

Direct benefits models of sexual selection.—In the “good resources” model, females select males that provide the greatest material benefit or the greatest amelioration of some reproductive cost, conferring an immediate contribution to fitness. Selection can favor males that directly provide valuable gifts to female or young (Wiggins and Morris 1986), or provide supportive territories (e.g. Searcy and Yasukawa 1983) or other defendable resources (Slagsvold 1986). Accordingly, the trait sexually selected itself has intrinsic nonarbitrary benefit or is a badge that honestly advertises a benefit. That makes it difficult to discern the degree to which such a trait is favored by (1) male mating success through sexual selection or (2) reproductive success through ecological selection (Andersson 1994). If habitat were sexually selected in this way, such habitat would be ecologically optimal, not merely ecologically acceptable. That would align habitat parameters favored by ecological and sexual selection, rendering ecological and sexual selection on habitat features concordant and, hence, indistinguishable.

Indirect benefits models.—Indirect sexual selection occurs where there is direct selection on a trait that is genetically correlated with the secondary sexual trait (Kokko et al. 2003). There are two principal mechanisms. The “Fisherian” or “runaway” model (Fisher 1930, O'Donald 1980) produces sexual traits that are nonadaptive, except with respect to mating. An initial advantage not due to sexual preference (*sensu* ecological selection) and a subsequent second advantage conferred by female preference conspire to concentrate in offspring both the preference and the trait. The intensity of such self-reinforcing selection increases so long as the sons of females exercising the preference

Box 1. How breeding habitat can be a sexually selected trait.

Consider a habitat matrix that consists of different proportions of two tree species, *A* (which is common) and *B* (which is uncommon). Species *A* is marginally better for foraging opportunities for both sexes of a hypothetical bird. At least one *B* is preferred in a male's territory, however, because the bark of *B* allows a female to make a superior nest.

Because *B* is uncommon, it is a resource that can drive evolution. The presence of a *B* tree in a territory could be (1) the initial niche advantage that benefits both sexes ("Fisherian" model), (2) an indicator that a genetically superior male in superior condition controls the territory ("good genes" model), or (3) a cue to males that females are likely to be attracted to the area ("territorial aggregation" model).

Under the Fisherian model, the coupling of males that commandeer *B* trees with females that prefer such males leads to runaway selection that increases the proportion of *B* trees in the selected habitat. Under the good genes model, the ability of genetically superior males to commandeer *B* trees constitutes a badge conveying high heritable viability, and females seeking superior males do so by selecting males whose territories have elevated proportions of *B* trees. Under the territorial aggregation model, males seeking mating opportunities do so by seeking areas where aggregations yielding additional chances are likely, and those are areas with elevated numbers of *B* trees. Under all three models, notwithstanding that *B* trees in excess provide no additional ecological benefits, or even render the territory sub-optimal ecologically, the preferred habitat rests at arbitrary and elevated proportions of *B* trees because of sexual dynamics. *B* trees become a sexy trait.

have an advantage over other males, and the trait develops to the point where some non-sexual disadvantage counterbalances the sexual advantage (Schluter et al. 1991).

A male tendency to obtain a territory in an advantaged habitat (*sensu* ecological selection) coupled to a female tendency to prefer such males could satisfy Fisher's two selective influences, generating sexually selected habitat. Both (1) the initial advantage conferred by the habitat trait and (2) the trait itself might be modest, but the latter could be multiplied many-fold by runaway selection stemming from the correlated preference trait. Countering ecological selection would prevent the narrowing of selected habitat parameters to points where the sexually selected habitat becomes excessively costly by being too rare, too unproductive, too narrowly circumscribed, or too excessively represented by the selected trait. Theoreticians do not agree on whether traits sculpted by Fisherian sexual selection are sustainable when female reproductive success is compromised (see Lande 1981, Kirkpatrick 1985, Pomiankowski et al. 1991, Day 2000). If not sustainable, this model could generate sexually selected habitat boundaries, but not ones that are costly to females.

The second indirect hypothesis is the "good genes" model: the sexually selected trait is costly but is coupled with some trait-enhancing survival. Females select costly male traits because they honestly signify high heritable viability (e.g. Zahavi 1975, Møller 1991, Petrie 1992; but see Brooks 2000), instead of being arbitrarily attractive as in Fisherian sexual selection. Although such indicators may also have nonsexual benefits (e.g. large size), ecologically selected and sexually selected optima are unlikely to be or remain the same, entailing a cost to sexual selection. Kirkpatrick (1996) showed theoretically that the good genes model can in some circumstances be costly for females, especially if countering ecological selection is weak.

For a sexually selected habitat trait to be an indicator of good genes, a correlation is required between heritable beneficial traits and a male's ability to settle in sexually prescribed habitat. That could be satisfied by male vigor; males most able to commandeer coveted sites would be those that can, in comparison with others, migrate earliest, defend best, display most effectively, and survive. By virtue of the specific habitat being a sexual commodity subject to competition, females' ultimate preference for good genes is mediated by a proximate preference for males occupying specific habitat. That system would select for and entrench that

specificity, with ecological selection tending to counter the development of excessively narrow habitat requirements.

Sensory drive and species recognition.— Ecological selection for sensory sensitivity to particular colors or shapes may produce a mating bias favoring sexual traits reminiscent of such colors or shapes (referred to as, among other names, the “sensory drive” model; e.g. Endler and Basolo 1998, Rodd et al. 2001). Sensory drive may be the “nudge” required to get a sexually selected system going (Kokko et al. 2003). Habitat parameters are much more complex than the colors or shapes exploited by sensory drive, however, making the sexually selected entrenchment of a particular breeding habitat through sensory drive unlikely. Although it is true that sexually selected traits like song frequency or plumage color can be dependent on environmental context (Hunter and Krebs 1979, Boughman 2002), that is not the same as suggesting that those traits determine environmental context by prescribing specific habitat.

In the “species recognition” model, it is contended that secondary sexual traits may be selected because they promote conspecific mate choice (Wallace 1889, Sibley 1957, Maynard Smith 1978). Regardless of the evidence, it is implausible that such a process could favor sexually selected habitat, because there are much better ways of recognizing a conspecific than assessing the habitat it occupies. Sexually selected habitat generated by other mechanisms may play a role in speciation or reproductive isolation, however. Ten Cate and Bateson (1988) suggested that assortative mating favored by diverging secondary sexual traits between populations could drive speciation. If one accepts the argument of Rice (1987) that sympatric speciation could flow from disruptive ecological selection on a habitat trait, there is no reason why disruptive sexual selection on a habitat trait could not similarly drive sympatric speciation.

Sexual conflict.— Evidence for sexual conflict, the divergence between male and female reproductive interests, has been accumulating (Parker 1979, Arnqvist and Rowe 2002, Chapman et al. 2003). Modeling indicates that such antagonism can prevent each sex from reaching sex-specific optima, reducing overall population fitness (Gavrilets et al. 2001). Sexual conflict can impair

female fitness if the optimal expression of a trait differs between the sexes (Rice and Chippindale 2001) or if a male trait increases the male’s paternity, notwithstanding that such increase may decrease a female’s reproductive output (Civetta and Clark 2000, Crudgington and Siva-Jothy 2000).

Sexual conflict can be facilitated by dimorphism under a “divergence in trait-optima” model. To the extent that morphology determines optimal habitat, such dimorphism could generate a sexual divergence in what constitutes optimal habitat. Different preferred winter habitats based on sex have been reported for passerines (Power 1980, Lynch et al. 1985). If habitat optima differ between the sexes, breeding habitat may reflect more the optimum of the controlling sex (presumably the choosing females) than that of the noncontrolling sex, entailing a cost to the latter. Accordingly, if during breeding the noncontrolling sex occupies the optimal habitat of the controlling sex, sexual dynamics are modestly influencing habitat choice. Ecological selection on the controlling sex and sexual selection (through conflict) on the noncontrolling sex prescribe specific breeding habitat.

The second conflict model that might affect habitat specificity is a “territorial aggregation” model, in which specific habitat is chosen not for resource exploitation but for the promotion of aggregation. Males commonly show substantially more variance than females in reproductive success (Clutton-Brock and Vincent 1991) through male-biased sex ratios (Stewart and Aldrich 1951, Smith 1978), polygyny, and especially extrapair copulations (Westneat et al. 1990, Møller and Cuervo 2000). Such nonmonogamous mating systems tend to affect female fitness qualitatively through female choice. In hidden leks (Wagner 1998), pursuit of extrapair males by females (Neudorf et al. 1997) selects for aggregations of male territories by rewarding males that tend to establish territories near other males (Hoi and Hoi-Leitner 1997).

Ecological selection is expected to concentrate male territories in habitat suitable for resource exploitation, but mate-choice rewards for females owing to such aggregation could narrow the habitat specificity. Because females seek access to multiple males to exercise choice, sexual selection will favor male traits that lead to aggregations, and the

narrowing of habitat parameters over which males compete could lead to such increased aggregation. Consequently, fitness benefits to females through access to superior males could entrench a sexually selected habitat (*sensu* sexual conflict) by virtue of the correlation between habitat specificity and such mating opportunities. Alternatively, if aggregation of male territories is driven not by females but by superior males, habitat specificity could be entrenched in a similar way.

Conclusions.—Although researchers continue to look to ecological selection as the primary explanation of habitat specificity, there is no *prima facie* reason why sexual selection might not influence breeding habitat preferences. Good resources, sensory drive, and species recognition models of sexual selection are unlikely to be primary forces in influencing habitat specificity in organisms. The “divergence in trait-optima” sexual-conflict model might modestly influence habitat specificity for one sex, though ecological habitat selection prevails through the other sex.

However, indirect sexual-selection models (Fisherian and good genes) and a “territorial aggregation” sexual-conflict model may be primary forces. In particular, such forces may work to generate habitat preferences that are not primarily mediated by the niche concerns of ecological selection. The significance of defending specific habitats when habitat is sexually selected is not that such territories provide resources in a manner superior to territories in alternative habitats, but that the habitat itself constitutes the currency of male competition and female choice.

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