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On the Possibility that Intercontinental Landbird Migrants Copulate En Route

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More than one-half of all North American landbirds undertake long-distance migrations between temperate breeding grounds and tropical wintering areas in the Caribbean Basin, Central America, and South America (Keast and Morton 1980). Although they spend over one-half of their annual cycle away from their breeding grounds, either en route or “wintering” in Neotropical areas, it is generally accepted that songbird migrants form pair bonds and copulate only after they arrive on their breeding grounds following spring migration (e.g. Nolan 1978). The occurrence of en-route copulations and perhaps even pair-bond formation prior to arrival on the breeding grounds has not been seriously considered by most ornithologists. If found, such behavior would have important implications for studying avian mating systems, testing assumptions and predictions of current sexual-selection models, and understanding the relationships among different phases of a migrant’s annual cycle.

This paper examines the possibility that copulations occur before migrants reach their North American breeding grounds. First, we address some of the obvious arguments against the premise that en-route copulations occur. We then describe some requirements, including anatomical and physiological, for copulations to have reproductive consequence. Finally, we discuss expectations and predictions if en-route copulations were to have reproductive consequences for male or female migrants. At the outset, it is important to distinguish between forming and maintaining a pair bond initiated during migration and en-route copulations. This paper does not directly address the former, but rather the general occurrence of en-route sexual behavior. We ask how likely is it that such behavior will have reproductive consequences, while assuming that a pair bond is formed with a mate shortly after individuals arrive on the breeding grounds (e.g. Nolan 1978).

Arguments against copulating en route.—The possibility that migrants copulate before they arrive on their breeding grounds has seemed unlikely because males commonly precede females during spring migration (e.g. Ramos 1988, Yunick 1988, Chandler and Mulvihill 1990), which decreases the probability that a male would encounter a female en route. Whereas the temporal pattern of migration may be sex dependent in spring, males and females do occur together at stopover sites (Francis and Cooke 1986) and overlap

exists in time of arrival on the breeding grounds (e.g. Nolan 1978, Eliason 1986; McDonald unpubl. data on Kentucky Warblers, *Oporornis formosus*). When migrants stopover along the northern coast of the Gulf of Mexico in spring, for example, small, homospecific groups of two or three individuals are common and often consist of both sexes (Moore et al. 1990).

On the wintering grounds, as well as during migration, observations of heterosexual pairs raise the possibility that some individuals form sexual bonds during migration before they arrive on the breeding grounds (Leck 1972, Morton 1980, Greenberg 1985, Greenberg and Gradwohl 1980, Moore et al. 1990, Morton pers. comm.). Speculation about early pair bonds has been influenced by the belief that most landbird migrants fly singly at night (Balcomb 1977), decreasing the probability that members of a pair could remain together during migration (e.g. Greenberg and Gradwohl 1980, Ramos 1988). Yet, recent observations of Prothonotary Warblers (*Protonotaria citrea*) suggest that homospecific groups sometimes depart on a spring trans-Gulf flight from the same location, maintain sufficiently close contact while flying at night to form a homogeneous flock the next morning, and stopover together on the northern coast of the Gulf of Mexico (Moore 1990). At the very least, the opportunity to copulate during migration exists.

Evidence to support copulation en route.—In order to prove that en-route sexual behavior could lead to fertilization of gametes, males must produce viable sperm and females must be shown to have sperm in their cloacas. The analysis of cloacal lavages (e.g. Quay 1984, 1985a, b, 1986a, b, 1989) has revealed that some males produce mature sperm during spring migration and far from their breeding grounds (e.g. Tennessee Warbler [*Vermivora peregrina*], Nashville Warbler [*V. ruficapilla*], Palm Warbler [*Dendroica palmarum*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*], and Painted Bunting [*Passerina ciris*]). Although the release of mature sperm is indicative of physiological readiness to breed, it need not be accompanied by ejaculation or copulatory behavior. Quay (1985b) suggested that the likelihood of sperm release in various species was related to breeding latitude and the brevity of the nesting season.

Quay (1989) found indisputable evidence that in at least one migratory species copulation occurs en route. Tennessee Warblers breed in southern Canada. Sperm were found in the cloacas of females as well as males

at Quay's study site in eastern Missouri, a minimum distance of 640 km from their breeding grounds. Although the presence of sperm in cloacal lavages from a female migrant is clear evidence of sexual behavior, including copulation, the resulting contribution, if any, to the male's or female's reproductive success remains unknown (i.e. the fate of those sperm vis-à-vis fertilization of female gametes). If early, en-route copulations are to have any relationship to fertilization of gametes, females must be capable of storing viable sperm for at least a few days and possibly a week or more. Uterovaginal sperm-storage tubules probably are ubiquitously distributed among birds (Shugart 1988, see also Hatch 1983, Bakst and Bird 1987, Birkhead 1988, Birkhead and Moeller 1992). The possession of sperm-storage tubules increases the probability of a female's maintaining viable sperm until she arrives on the breeding grounds (i.e. until eggs can be fertilized or until sperm transferred en route are replaced with the sperm of another male). Ovulation may occur shortly after arrival on the breeding grounds, notably among females breeding at higher latitudes. McDonald (unpubl. data), for example, found for color-banded Kentucky Warblers in Virginia that females have initiated nest building shortly after arrival and have laid their first viable eggs as early as eight days after arrival on the breeding grounds. Whereas scant information exists on sperm storage, sperm competition, and the frequency with which females lay infertile eggs due to inadequate access to sperm, it appears that duration of sperm storage is linked with the ecology of the species (see Birkhead 1988), and existing evidence suggests storage capability on the order of two weeks or longer (Birkhead et al. 1989, Birkhead pers. comm.).

Singing during migration is indicative of both the physiological and behavioral changes beginning to occur in readiness for breeding. Although song may be epiphenomenal when sung en route, its role in attracting transitory partners for copulation deserves investigation. Black-throated Green Warblers (*Dendroica virens*), for example, sing their "accented ending" songs during migration, which are typically sung in intersexual contexts during the breeding season (Morse 1989, 1991).

Advantages of en-route sexual behavior.—Besides the possibility that en-route copulations may be "for practice" or the passive consequence of sexual maturation or gonadal recrudescence, the advantages of en-route sexual behavior that results in disseminating viable sperm are more obvious for male migrants. Because of constraints associated with the restricted breeding season of the Temperate Zone (e.g. Slagsvold et al. 1988, Morton et al. 1990), efforts to copulate en route may represent an alternative reproductive strategy for males who are not likely to secure breeding opportunities on the breeding grounds because they arrive too late to establish a territory or attract a mate. Younger males are more likely to migrate later than

older males, arrive later on the breeding grounds, and (if unable to attract a mate) experience reduced reproductive success (e.g. Morton and Derrickson 1990). Coincidentally, younger males are more likely to overlap with females at stopover sites (Kuenzi 1989, Moore unpubl. data).

Of course, the probable decline in the ability of sperm to compete with sperm from a male that a female copulates with subsequently has important implications for males that may use copulations prior to the breeding season as a reproductive strategy. An early copulation (i.e. relative to when eggs are fertilized) may not confer any reproductive advantage even if sperm transferred during migration are not replaced by another male's once the female arrives on the breeding grounds (Birkhead 1988). However, until more is known about the viability and longevity of stored sperm, we cannot discount the possible benefit of en-route copulations to male or female migrants.

The possible advantages of en-route copulations are less clear for females (cf. Westneat et al. 1990). If males are unable to force copulation with females (e.g. Rohwer 1978; but see Westneat 1988, Morton 1987, Morton et al. 1990), the stability of a male's mixed strategy is contingent upon the female's willingness (or indifference) to copulate (Fitch and Shugart 1984). Given that multiple mating by females on the breeding grounds can be frequent (Fitch and Shugart 1984, Birkhead et al. 1987, Westneat 1988), what advantages might en-route copulations confer upon females? First, a female migrant might engage in copulations during migration to hedge her bets against the possibility of either not acquiring a mate upon arrival, or acquiring a "low-quality" mate. Females of long-distance migratory species may be more constrained in their choice of mates upon arrival than previously supposed (see Eliason 1986, Slagsvold et al. 1988, Alatalo et al. 1989). The suitable breeding season may be relatively brief, especially at higher latitudes. The prospects of successfully raising one clutch, and especially a second or third clutch, will decline over time (Alatalo and Lundberg 1984, Eliason 1986). Consequently, females should make their mating decisions quickly upon arrival on the breeding grounds because time spent searching for a mate is costly. If time constrains mating opportunities for females on the breeding grounds, some genetic advantage may accrue to females who copulate en route. A time-constrained female might also gain an additional, nongenetic advantage from en-route copulations, namely the assessment and acquisition of new mates (e.g. Colwell and Oring 1989, Wagner 1991). A female that copulates during migration also derives the advantage, if any, of an extrapair copulation while avoiding costs that may accrue from an extrapair copulation on the breeding grounds, such as reduced mate assistance or desertion (e.g. Fitch and Shugart 1984).

A second, nongenetic advantage that en-route cop-

ulations might confer to females is that accepting a persistent male may be less costly than resisting, assuming copulation is not especially prolonged or conspicuous. She may have the option to remate later and "replace" sperm transferred en route (see Alatalo et al. 1989, Austad 1984). This indifference may be especially valuable at migratory stopovers when time spent avoiding a persistent male would conflict with foraging priorities and the avoidance of predators (see Loria and Moore 1990). In any case, any negative reproductive consequences of copulating with a persistent male are probably not severe if the female can shed sperm or if last-male sperm precedence exists (e.g. Compton et al. 1978).

A female that copulates en route helps to ensure the presence of a sufficient quantity of sperm in her oviduct or cloaca for fertilization. If variation in fertility among breeding males is high or if it is difficult for females to discern variation in male fertility, arrival on the breeding grounds with some sperm could allow females to overcome infertility of her mate.

Conditions and some predictions.—If copulations during migration transfer sperm that have a reasonable chance of fertilizing eggs, we would expect several conditions to hold regarding anatomy, physiology, and behavior. (1) Males must produce viable sperm in measurable quantities during migration. (2) If sperm production or if attempted copulations are shown to be physiologically and energetically expensive, such information would lend more support to the hypothesis that copulating en route can be advantageous. (3) Females that copulate en route should be capable of storing sperm and arriving on the breeding grounds with viable sperm. (4) If sperm longevity is less than the time spent en route, copulations should be more common nearer the breeding grounds. (5) If en-route copulation is favored because time for mate selection is limited on the breeding grounds, the frequency of en-route copulations should be higher among populations characterized by relatively short breeding seasons (e.g. those breeding at higher latitudes). (6) If attempting copulations during migration is time consuming or increases the risk of predation, en-route copulations should be more characteristic of younger birds (e.g. second year), or those that are otherwise less likely to acquire a mate on the breeding grounds. (7) Females that may appear to a male as "low quality" (e.g. first year) should seek or be more receptive to en-route copulations. (8) The frequency of en-route copulations or other evidence of mating behavior, including intersexual song and courtship activity, should be correlated with the quality of stopover habitat (sensu Moore and Simons 1992).

In this paper we have summarized evidence consistent with the possibility that landbird migrants copulate en route and suggested how early copulations might confer a reproductive advantage to males and females. Unfortunately, little is known about the behavior of migrants during stopover, and what we

do know is understandably related to nutritional constraints. Yet, our understanding of mating systems among migratory passerines and the application of current models of sexual selection to these species clearly are affected by the possibility raised in this commentary.

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