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OVERVIEW

TREE SWALLOWS (*TACHYCINETA BICOLOR*): A NEW MODEL ORGANISM?

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THE TREE SWALLOW (*Tachycineta bicolor*) has been the focus of a diversity of research that is rivaled by few other bird species. A quick search through the Science Citation Index reveals over 400 manuscripts either focusing on or involving Tree Swallows in the last 25 years, on topics ranging from mating systems to nest-building behavior, from climate change to environmental contamination. Here, I focus on two themes: (1) the Tree Swallow as a "new" model organism, and (2) Tree Swallow research findings that have important implications for all avian biology and, indeed, biology in general.

THE TREE SWALLOW AS A "NEW" MODEL ORGANISM

To appreciate the diversity of research undertaken with Tree Swallows, we must first understand why so many researchers use Tree Swallows as their focal organism. Model organisms tend to have four features in common: rapid development and short generation time, small adult size, ready availability, and tractability (Bolker 1995). Whereas the Tree Swallow falls a little short on the first two compared to traditional model organisms, the fact that this species readily breeds in nest boxes makes it about as available and tractable a study organism as any avian biologist could hope for. That feature allows researchers to set population sizes, control external perturbations (e.g. predation), as well as standardize and manipulate nest-site characteristics and contents (e.g. cavity volume, brood manipulations). In addition, the ease with which individuals can be captured and uniquely marked greatly facilitates research activities. All those factors combine to allow researchers flexibility unavailable with most other bird species. In fact, I would argue that Tree Swallows deserve equal standing beside fruit flies, nematodes, and mice as one of the classical model organisms in biology.

WHAT HAVE WE LEARNED FROM THE TREE SWALLOW?

Tree Swallow research has covered a highly diverse array of subjects including extrapair paternity (Lifjeld and Robertson 1992, Lifjeld et al. 1993), infanticide (Robertson 1990), delayed plumage maturation in females (Stutchbury and Robertson 1987a), costs of reproduction (Wheelwright et al. 1991), senescence (Robertson and Rendell 2001), climate change (Dunn and Winkler 1999), and pollution (McCarty and Secord 1999a, b), to name just a few. Given this breadth, I could not hope to do it all justice in this article. As a consequence, I have selected two areas of Tree Swallow research that I feel have had an important influence on avian biology—mating systems and reproductive behavior, spatial relationships and individual movements; and two areas whose influence is just beginning to be felt—timing of life-history events relative to climate change, indicators of environmental contamination.

MATING SYSTEMS AND REPRODUCTIVE BEHAVIOR

Extrapair paternity and mate choice.—Extrapair paternity is now widely recognized as a frequently occurring phenomenon among socially monogamous birds (e.g. Griffith et al. 2002). The extent of extrapair paternity in a population depends on interactions among three individuals: the extrapair male and his ability to obtain extrapair copulations, the social male and his ability to protect paternity in his nest, and the female and her proclivity for seeking extrapair copulations (Westneat et al. 1990, Dunn et al. 1994a). Extrapair paternity appears to be more common in Tree Swallows than in most other species; 50–90% (Dunn et al. 1994a) compared to an average of 14% for other species (Birkhead and Møller 1992), a high frequency that is not an artifact of nest boxes (Barber et al. 1996). In addition, the prevalence of extrapair paternity also varies widely between years within a breeding

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population (e.g. 50% of broods in one year, 87% the next) and between individuals within a single population (Dunn et al. 1994a). Those factors, when combined with the ability to capture and sample complete family groups, have allowed Tree Swallow researchers a unique opportunity to examine the relative strengths of the three players in the extrapair mating game.

Perhaps the most interesting finding of Tree Swallow extrapair research is that extrapair copulations are almost completely under the control of the female (Venier and Robertson 1991, Lifjeld and Robertson 1992, Venier et al. 1993, Dunn et al. 1994b). In fact, female preference appears to override most other factors that have the potential to influence the opportunity for extrapair activity (e.g. nest-box location, nest-box density, breeding synchrony, experience; Dunn et al. 1994b). However, there are no consistent across-year patterns with respect to the characteristics of males selected by females (e.g. size, experience, arrival date) that allow the clear definition of a high-quality mate (Dunn et al. 1994a, Barber et al. 1998, Conrad et al. 2001). Indeed, one could conclude from those studies that the definition of a high-quality mate is not a fixed definition; rather, it may change both with and among breeding seasons as ambient conditions change (e.g. weather, food availability, talent pool).

Importance and role of floaters.—Whenever breeding resources are limited, there is a potential for a proportion of a population to be unable to breed despite being reproductively mature (e.g. Brown 1969, Smith 1978). In some species, such as the Tree Swallow, that proportion can be quite large (Stutchbury and Robertson 1985). As a consequence, understanding the role of floaters can be an important component of understanding a species' population dynamics.

There are at least three theories concerning the characteristics of floating individuals. The first theory contends that floating individuals are younger or competitively inferior individuals or both who were unable to obtain a breeding opportunity (e.g. Shutler and Weatherhead 1992). The second theory contends that individuals choose to forego breeding in the hope of obtaining a high-quality nest site or territory should one come available (e.g. Zack and Stutchbury 1992). The third theory contends that floating is a viable alternative reproductive strategy to holding and defending a nest-site or breeding territory. For females, that could take the form of intraspecific brood parasitism (Gowaty 1985, Sandell and Diemer 1999); for males, extrapair paternity (Petrie and Kempenaers 1998).

Tree Swallows, as secondary cavity nesters, are often strongly nest-site limited (Holroyd 1975). As a consequence, there are always individuals of both sexes who are unable obtain to nest sites or mates or both. Female Tree Swallows do not reproduce until they can obtain a nest site (Stutchbury and Robertson 1987b); intraspecific brood parasitism is very uncommon in this species (Lombardo 1988, Barber et al. 1996, Kempenaers et al. 1999). Most female floaters are one-year-old females (Stutchbury and Robertson 1987b) who do not breed although they do spend a considerable amount of time prospecting for nest sites.

The Tree Swallow is one of only two species in North America in which only the female and not the male displays delayed plumage maturation (Hussell 1983, Stutchbury and Robertson 1987a; the other is the Hooded Warbler [*Wilsonia citrina*], Morton 1989). Subadult Tree Swallow females have a dull brownish plumage that contrasts strongly with iridescent blue plumage of adult males and females (Hussell 1983). Stutchbury and Robertson (1987a) hypothesized that the distinctive plumage of subadult females served to reduce aggression by resident males (sexual signaling) and resident female (subordinate signaling), thereby facilitating exploration. Resident males tended to be less aggressive to subadult females than to intruding adult females, whereas resident females were equally aggressive towards subadult and adult intruders. Those results and others (Lozano and Handford 1995) imply that female subadult plumage is primarily an intersexual signaling adaptation.

Unlike female floaters, however, male floaters are able to obtain a modest degree of reproductive success despite not defending a nest box. In one study (Kempenaers et al. 2001), floaters were responsible for 13% of extrapair young to which the researchers could assign paternity. Again unlike females, there were few differences—morphological or otherwise—between floater and resident males, other than a tendency for males who participated in extrapair matings (including floaters) to be heavier than those that did not. That study supported previous observations that male floaters participate in extrapair copulations (Barber and Robertson 1999), but was one of the first to document successful reproduction by floaters in any passerine species (see Ewen et al. 1999).

Mate guarding, paternity confidence, paternal care, and infanticide.—Ever since researchers confirmed the existence of extrapair mating strategies in birds, there has been an interest in (1) whether or not males can prevent females from engaging in extrapair activity and vice versa, and (2) whether or not males can tell if there are extrapair young in their own nests. Male birds employ several behaviors in an attempt to minimize the extrapair activity undertaken by their social mate. First, they can attempt to prevent the settlement of conspecific pairs nearby (Rendell and Robertson 1994). Second, they can maintain visual vigilance over their social mate and interrupt any extrapair activity (Birkhead 1979). Third, males may attempt to copulate with their social mate as frequently as possible to win the sperm competition battle (Birkhead et al. 1989). Research into those behaviors in Tree Swallows has led to the conclusion that male behavior is largely dictated by female activity (Chek and Robertson 1994, Whittingham et al. 1994). Given that female Tree Swallows appear determined to participate in extrapair activity, frequent copulation may be a more efficient strategy to insure paternity than is intense following (Venier and Robertson 1991, Whittingham et al. 1994); it is less energetically costly and provides the male opportunities to pursue his own extrapair activities. However, given the prevalence of extrapair young in Tree Swallow nests (Lifjeld et al. 1993), it appears that whatever strategy males adopt are not particularly effective. Indeed, mate guarding (either by following or frequent copulation) may only be a viable paternity confidence strategy when females have little interest in pursuing extrapair activities (Chek and Robertson 1994).

How males ascertain the presence of extrapair young in their nests is unclear. Because it is difficult to test nestling recognition by males directly in the field, we need to identify behaviors that are proxies for paternity confidence. One obvious candidate is male parental care. Building on parental-investment theory which predicts a decrease in male parental care with a decrease in paternity confidence (Trivers 1972), Whittingham et al. (1992) outlined a theoretical framework for the trade-offs among paternity confidence, male parental care, and offspring recruitment. In species such as the Tree Swallow, where male care positively affects offspring recruitment (Leffelaar and Robertson 1986), one would predict a positive relationship between paternity confidence and male parental care; the shape of the curve depends on the strength of the relationships between care and recruitment. In Tree Swallows, empirical evidence indicates that paternity confidence appears to have little effect on male parental care unless the probability of paternity is very low (Robertson 1990, Whittingham et al. 1993); that matches findings for other socially monogamous species (e.g. Indigo Bunting [*Passerina cyanea*]; Westneat 1988). There are at least two reasons for that lack of a relationship. One is that males are unable to assess the proportion or likelihood of extrapair young in their nests, except in extreme cases. If that is the case, then it behooves males to continue caring for nestlings on the chance that some of them are theirs. Alternatively, males may feel "confident" in their guarding behaviors such that they have no need to question the paternity of their brood. Females may bolster that confidence by soliciting and accepting copulations from their social mates after absences from the nest site (Kempenaers et al. 1998).

Another alternative avenue to examine a male's ability to assess paternity is to perform a removal experiment (i.e. remove the resident male) and monitor the behavior of the replacement male. Removal experiments with Tree Swallows have led to some interesting and startling results concerning the lengths that males will go to insure paternity (Robertson and Stutchbury 1988, Robertson 1990). If a male is removed during the egg-laying stage, the replacement male tends to adopt the brood, because there is a probability that he has at least partial paternity (Roberston 1990). Replacement males that arrive after clutch completion but early in incubation tend to adopt the brood whereas males that arrive late in incubation tend to commit infanticide, killing the nestlings after they hatch to induce the female to renest. Similarly, replacement males that arrive during the nestling stage almost always commit infanticide (Robertson and Stutchbury 1988, Robertson 1990). Infanticide in Tree Swallows appears to be a sexually selected behavior. Unmated males that are infanticidal are able to obtain a breeding opportunity and, hence, will have a higher potential fitness than unmated males that are not infanticidal (Robertson and Stutchbury 1988, Robertson 1990).

Females are not passive by-standers in that somewhat macabre scenario. Females tend to be receptive to replacement males during egg-laying and incubation and may attempt to pacify the replacement males by readily accepting copulations (Robertson 1991). However, when the replacement male arrives during the nestling stage, females react very aggressively to their presence and may, in some cases, be able to prevent infanticide (Robertson 1991). Interestingly, female Tree Swallows are also known to commit sexually selected infanticide, likely driven by nest-site limitation (Shelley 1934, Robertson and Stutchbury 1988, Chek and Robertson 1991). Chek and Robertson (1991) removed four females during incubation and four during the nestling stage. All the incubation replacements buried the existing eggs with a new nest and laid their own clutch. Only two of the four experimental nestling-removal boxes received a replacement female. One of those females ignored the nestlings until they died; the dead nestlings disappeared from the nest box and she started her own clutch. The second replacement female committed infanticide.

Spatial Relationships and Individual Movements

Nest-site competition drives a large proportion of Tree Swallow reproductive behavior. It also shapes the spatial relationships exhibited by nesting birds and dispersing individuals. Nesting Tree Swallows exhibit a distinct concept of personal space. In both natural cavities and nest-box grids, nesting pairs attempt to nest as far from other pairs as possible (Robertson and Rendell 1990) and will attempt to prevent conspecifics from nesting in close proximity (Muldal et al. 1985, Lombardo 1987), often by concurrently defending two or more nest sites (Harris 1979, Robertson and Gibbs 1982, Rendell and Robertson 1989). The benefits of extranest defense are likely sex-specific. For males, defending extra sites may increase the probability of attracting a second mate (resource defense polygyny, Dunn and Hannon 1991, Rendell and Robertson 1994). Resident females, on the other hand, may defend extra sites to achieve the opposite result, namely to prevent settlement of other females, thereby minimizing a male's opportunity for extrapair activity (Rendell and Robertson 1994). In addition, females may defend extra nest sites to facilitate re-nesting in the event of a nest failure. Those results provide interesting insights into the potentially conflicting motivations behind male and female territoriality and resource defense.

So, what about after the breeding season? The decision whether or not to disperse, for both adults and juveniles, is ultimately based on a cost–benefit analysis. By dispersing, an individual is entering an unknown area, giving up information on resource availability, predator abundance, and possibly mating opportunities. On the other hand, a dispersing individual may find abundant resources and better mates (Clobert et al. 2001). For adult birds, it has been hypothesized that a poor breeding season should motivate individuals to find greener pastures (Greenwood and Harvey 1982). However, empirical evidence suggests that is not always the case (e.g. Lindberg and Sedinger 1997), although the reasons for that are unclear. Even less clear are patterns and motivators behind natal dispersal (but see Brown 1987).

Tree Swallows provide a perhaps unique opportunity to examine both adult and juvenile dispersal. Individuals are easily captured and marked which facilitates measurements of internest movements and shows reasonably high local and regional site fidelity (reviewed in Robertson et al. 1992), thereby improving sample sizes for analytical purposes. Shutler and Clark (2003) took advantage of those factors in their long-term study (12 years) of adult and natal dispersal in Tree Swallows. They tested three sets of relationships: between breeding success and adult dispersal; among manipulated clutch size, adult dispersal, and natal dispersal; and between breeding success and dispersal distance. Contrary to their predictions, however, neither adult nor natal dispersal distances were related to breeding success, nor did manipulating breeding success affect dispersal. Furthermore, dispersal distance had no significant effect on breeding success the following year. Shutler and Clark (2003) hypothesize that because, in most years, most nests produced at least some breeding success (i.e. at least one fledgling) and because individual nest sites did not consistently produce high breeding success, individuals would have little to gain by moving to a new site. In addition, because individuals appear to be highly box-faithful between years (Robertson et al. 1992, Shutler and Clark 2003), the influence of social interactions on site fidelity and dispersal cannot be discounted.

Timing of Life History Events Relative to Climate

There is a growing body of evidence detailing ecological effects of global warming on the earth's biota (e.g. Ottersen et al. 2001). Trends uncovered in the bird world include the advancement of egg-laying (Crick et al. 1999), desynchronization of onset of breeding and food abundance (Visser et al. 1998), and alteration of population growth rates (Sæther et al. 2000). However, most of that bird research has been undertaken in Europe and long-term or large-scale studies are rare in North America (for notable exceptions see Brown et al. 1999 and Nott et al. 2002). Tree Swallows provide a useful model for examining large-scale phenomena in North America (see Winkler et al. 2002), given their continent-wide range and the ease with which breeding activity can be monitored. Recently, Dunn and Winkler (1999) published an analysis of 3,450 Tree Swallow nest records collected over 40 years (1952–1992) across North America. They uncovered an advancement of five to nine days in egg-laying date that they associated with increasing air surface temperatures during the breeding season and, given the scope of their sampling, reasonably concluded that this trend toward earlier breeding likely encompasses all Tree Swallows breeding in North America.

However, there is some evidence that climate change may not affect all aspects of a species' range in a similar manner (Visser et al. 1998) and that climate patterns themselves also exhibit significant spatial variation (Easterling et al. 2000). With that in mind, Hussell (2003) presented results of a long-term study (1961–2001) of Tree Swallows nesting on and near Long Point, Ontario, an area not covered by Dunn and Winkler's (1999) sampling. Hussell's (2003) results indicate that although spring temperatures were an important predictor of the timing of egg laying, there was no evidence for increasing spring temperatures in the Long Point area. As a consequence, the effect of changing spring temperatures on Tree Swallow breeding would be best appreciated as a regional, rather than continental, phenomenon. That finding has important implications for the examination of the effects on birds of other widespread phenomena (e.g. El Niño Southern Oscillation, hemlock woolly adelgid [Adelges tsugae] outbreaks).

Environmental Contamination

The detrimental effects of environmental contaminants created as a by-product of human activity have long concerned scientists and environmentalists. Partly due to their charismatic nature, birds and the negative effects of contaminants on them have been the focus of ecotoxicology research for many years. For example, population declines of birds were the first indicators of environmental contamination by lead (Grinnell 1894), pesticides (Carson 1962), and polychlorinated biphenyls (PCBs; Jensen et al. 1969).

Of environmental contaminants, PCBs are among the most widespread and well studied. One area of specific interest is the magnitude and regularity of transfer of PCBs from sites of deposition in aquatic systems into terrestrial ecosystems and food webs. Recent research has focused on Tree Swallow behavior and reproductive performance as an index of that uptake and transfer from aquatic to terrestrial systems (McCarty and Secord 1999a, b; Golden and Rattner 2003).

Tree Swallows have the potential to be an effective indicator species for PCB contamination: they are abundant and their biology is well understood (Robertson et al. 1992); they nest willingly in nest boxes; and they feed largely on insects with aquatic larval stages, thereby potentially providing an assay of aquatic contamination and biomagnification (Bishop et al. 1995, McCarty and Secord 1999b, Secord et al. 1999). Furthermore, there is a large body of evidence that PCBs accumulate in eggs and bodies of nestlings and adults (e.g. Custer et al. 2002). However, the ultimate utility of the Tree Swallow as a bioindicator will depend on the ability of researchers to accurately describe natural variation (i.e. baseline variation) in the trait they wish to use as the indicator (e.g. population size, breeding success) to accurately measure a response to a perturbation (Cottingham and Carpenter 1998).

CONCLUSION

As I began my graduate career, I recall regularly chiding my dissertation supervisor about his choice of study organism. How could you possibly find satisfaction studying a box-nester? Where is the challenge in studying the avian equivalent of a white rat? Well, as I struggled through my studies and the small samples sizes and ecological noise created by my own choice of a model organism, I learned a valuable lesson about being seduced by the appeal or attractiveness of a study organism. The Tree Swallow may not be the most glamorous model organism, but it has certainly proven to be one of the most productive in avian biology.

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