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Individual and Seasonal Variation in External Genitalia of Male Tree Swallows

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ABSTRACT.—The cloacal protuberance (CP) of passerines functions primarily to store spermatozoa. When gently squeezed, the CP of male Tree Swallows (*Tachycineta bicolor*) everts to expose a small papilla from which semen can be expressed. From 1994 to 1999, I examined individual and seasonal variation in CP dimensions and papilla length of mated male Tree Swallows in western Michigan. Male CP volumes were greatest when their mates were laying eggs and declined to the nestling period. Papilla lengths did not vary over the course of the breeding season. Cloacal protuberance dimensions and papilla length were not associated with the age class of a

male's mate, the date she started laying eggs, or number of eggs she laid. The decrease in CP size over the course of the breeding season is consistent with the steady decrease in reproductive opportunities for male swallows. Although it seems likely, whether or not the papilla of Tree Swallows functions as an intromittent organ awaits further study of the anatomical mechanics of copulation in these birds.

During the breeding season, the distal ends of the ductus deferens (seminal glomera) of male passerines fill with newly formed spermatozoa resulting in a swelling of the cloaca commonly referred to as the cloacal protuberance (CP) (King 1981). The CP can be considered as the external male genitalia. The di-

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mensions of animal genitalia are often a reflection of consequences of sexual selection (Eberhard 1985).

The CP of passerine birds functions primarily to store spermatozoa (Wolfson 1952, 1954a, b, Salt 1954), although it may also facilitate copulation in some species (Mulder and Cockburn 1993, Birkhead and Hoi 1994, Sax and Hoi 1998). Wolfson (1960) suggested that the CP might act as a phallus transferring sperm, or in some other way facilitate copulation. Cloacal protuberance dimensions vary in size over the course of the breeding season (Wolfson 1954a) relative to male reproductive condition. The observation that CP dimensions vary with reproductive opportunities (Sax and Hoi 1998) implies that expression of that trait can be molded by the selective pressures resulting from sperm competition (Birkhead and Møller 1992, Briskie 1993).

Passerines with large CP tend to have large seminal glomera that store many sperm cells (Briskie 1993) in anticipation of sperm competition (Birkhead and Møller 1992, Briskie 1993). Thus, interspecific variation in CP dimensions reflects variation in levels of sperm competition among species (Briskie 1993, Tuttle et al. 1996, Sax and Hoi 1998).

Tree Swallows (*Tachycineta bicolor*) have some of the highest levels of extra-pair paternity recorded in passerines, with up to 87% of nests (Barber et al. 1996, Kempenaers et al. 1999) containing from 25 to 100% extrapair young (Barber et al. 1996, Fig. 2). This pattern of extrapair paternity and the fact that females have sperm storage tubules (Shugart 1988) implies that sperm competition is an important component of Tree Swallow reproductive biology and sets the stage for sexual selection on traits that would increase a male's chances of winning in sperm competition. The high frequency of extrapair paternity and within-pair copulations (Venier and Robertson 1991) favors enlarged CP dimensions in Tree Swallows (Birkhead et al. 1993). Indeed, male Tree Swallows have disproportionately large testes, and the number of sperm in the seminal glomera is positively correlated with CP volume and seminal glomera mass (Peer et al. 2000). When gentle pressure is applied to its sides, the cloaca of male Tree Swallow everts exposing a red, pyramidal shaped phallus-like papilla and semen can be expressed from its tip, suggesting that it might function as an intromittent organ (but see Briskie and Montgomerie 1997).

The objectives of this study were to (1) assess individual and seasonal variation in CP dimensions and papilla length, (2) examine the relationship between CP dimensions and papilla length and male body size and reproductive performance, and (3) evaluate whether CP dimensions reflect seasonally dependent male reproductive opportunities as demonstrated for Bearded Tits (*Panurus biarmicus*) by Sax and Hoi (1998).

Methods.—From 1994 to 1999, I measured CP dimensions of male Tree Swallows that bred in some of the 100 wooden nest boxes mounted on metal poles

erected in grids in an old field on the campus of Grand Valley State University, Ottawa County, Michigan, USA 42°57'N, 85°53'W. Each year, I began monitoring breeding activity and reproductive performance on 1 May, although swallows arrived well before that date. No clutches were initiated before 1 May. I used plumage characteristics to categorize females as either second-year (SY, mostly brown dorsal plumage) or after second-year (ASY, mostly iridescent blue-green dorsal plumage) (Hussell 1983) because SY and ASY females can differ in reproductive performance (Stutchbury and Robertson 1988). Females in intermediate plumage were categorized as after hatching year (Hussell 1983). Males develop the full adult breeding plumage before their first winter (Dwight 1900).

I captured males at their nest boxes at various times during the breeding cycle (i.e. egg-laying, incubation, and nestling periods). On each male, I measured the height of the CP from the anterior ventral surface of the lower abdomen to the tip of the cloaca and its left-to-right diameter at its tip to the nearest millimeter using a ruler rather than calipers to avoid compressing the CP and distorting its shape and size. Cloacal protuberance volume (cubic millimeters) was calculated as $\pi \times \text{height} \times (\text{diameter}/2)^2$, assuming a cylindrical shape (Kempenaers et al. 1999). I also measured tarsus, bill, tail, and wing chord length and asymmetry; determined mass; and scored each bird for ectoparasites (see Lombardo and Thorpe 2000 for details). To avoid pseudoreplication, every individual was measured only once each breeding season. I used the mean measurements for tarsus and bill lengths to examine relationship between those morphological features and cloacal protuberance size and papilla length for males measured multiple times from 1994 to 1999. I used yearly measurements for wing chord length and asymmetry, tail length, weight, and ectoparasite scores to examine relationship between those morphological features and cloacal protuberance size and papilla length because the size of those features is likely to vary from year to year with variation in individual condition.

To examine relationship between CP volume and body size, I calculated CP volume index (CP volume/body mass; cubic millimeter/gram⁻¹) following Birkhead et al. (1991). I did not correct individual CP volumes for body-mass differences because there were no differences ($F = 1.25$, $df = 2$ and 263 , $P = 0.29$) among males in mean mass while their mates were either egg laying (20.87 ± 1.13 (SD) g, $n = 63$), incubating eggs (20.68 ± 1.10 g, $n = 30$), or tending nestlings (20.60 ± 1.22 g, $n = 173$). Cloacal protuberance volume index was not mentioned further because subsequent analyses showed that results of analyses that used CP volume and CP volume index were similar.

From 1995 to 1999, I measured length of papilla on each male from where it emerged from the everted cloaca to its distal terminus to the nearest millimeter using a ruler rather than calipers. I used enough pressure on the sides of the CP so that the papilla

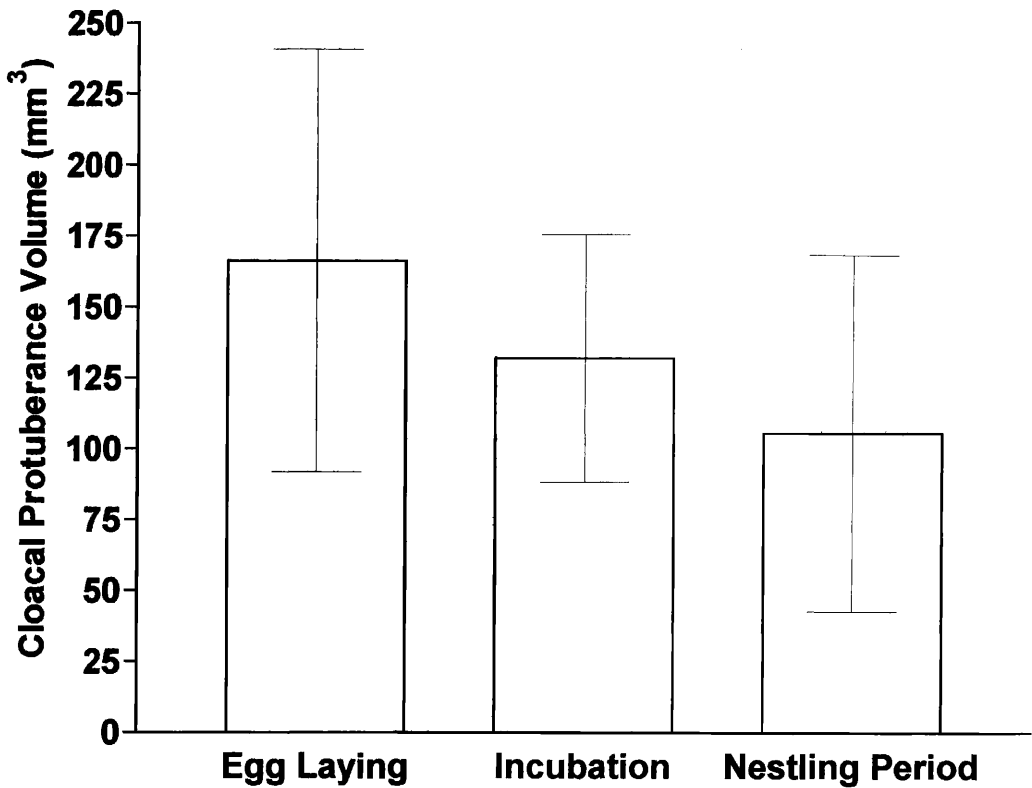


FIG. 1. Mean male Tree Swallow cloacal protuberance volume (cubic millimeter) varied with stage in breeding season; egg laying ($n = 63$), incubation ($n = 31$), and nestling period ($n = 157$). Means \pm SD are indicated.

was maximally emerged from the urodeum of the cloaca (King 1981, Lake 1981).

I banded each swallow with a numbered Federal aluminum band and gave it a unique color mark to facilitate individual identification on its breast, tail, throat, or wing feathers using water-proof marking pens and acrylic paints.

The data were analyzed using SPSS 8.0 for Windows (SPSS 1997).

Results.—The volume of the CP of mated male Tree Swallows varied over the course of the breeding season and was greatest when their mates were laying eggs and declined to the nestling period (Kruskal-Wallis test, $\chi^2 = 41.6$, $df = 2$, $P < 0.001$) (Fig. 1). The decrease in CP volume resulted from decreases in both CP height ($\chi^2 = 10.34$, $df = 2$, $P < 0.001$) and CP diameter (Kruskal-Wallis test, $\chi^2 = 40.93$, $df = 2$, $P < 0.001$). There were no significant correlations between CP volume and date when their mates were laying or incubating eggs when each stage of the nesting cycle was considered separately, but CP volume significantly decreased with date when males were tending nestlings (Spearman's rho, $r_s = -0.59$, $n = 132$, $P < 0.001$). Over the course of the whole

breeding season, CP volume significantly decreased with Julian date (Fig. 2).

The CP volumes of males mated to ASY (123.84 ± 69.41 mm³, $n = 190$) and SY females (133.67 ± 72.83 mm³, $n = 41$) were not significantly different (Mann Whitney *U*-test, $U = 3503$, $P = 0.31$).

The papilla of male Tree Swallows varied from 2–5 mm in length (mode = 3; Fig. 3). A disproportionate number of males (134/212, 63%) had a papilla 3 mm in length (Kolmogorov-Smirnov test, $Z = 4.96$, $n = 213$, $P < 0.001$). Papilla length was independent of the stage in the breeding cycle when it was measured ($\chi^2 = 5.11$, $df = 4$, $P = 0.28$; Fig. 3). Papilla length categories 4 and 5 mm were pooled in this analysis because there were only a few males in the 5 mm category (Fig. 3). There was no correlation between papilla length and date (Pearson's $r = 0.06$, $n = 169$, $P = 0.43$). Papilla length was independent of the age class of a male's mate ($\chi^2 = 3.07$, $df = 2$, $P = 0.22$). The mean papilla lengths of males mated to ASY (3.08 ± 0.64 mm, $n = 162$) or SY females (3.26 ± 0.73 mm, $n = 31$) were not significantly different ($U = 2163$, $P = 0.16$).

There were no significant correlations between CP volume and papilla length (all $P > 0.05$) during each

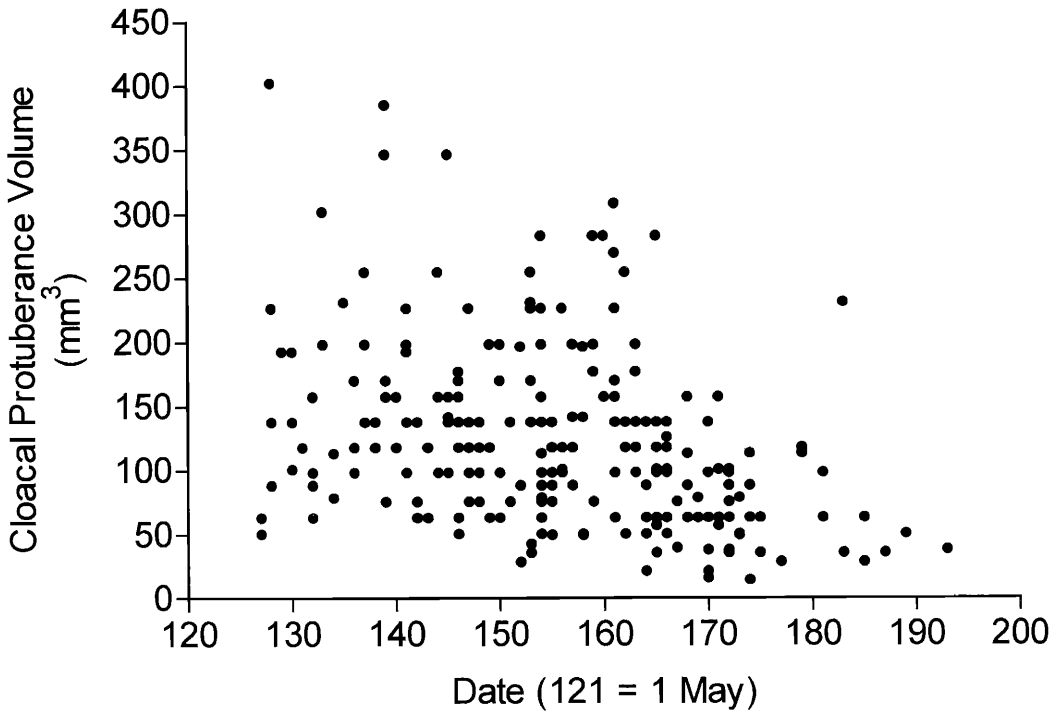


FIG. 2. Male Tree Swallow cloacal protuberance volume (cubic millimeter) decreased with the Julian date when the protuberance was measured; Spearman's rho = -0.59, $n = 208$, $P < 0.001$.

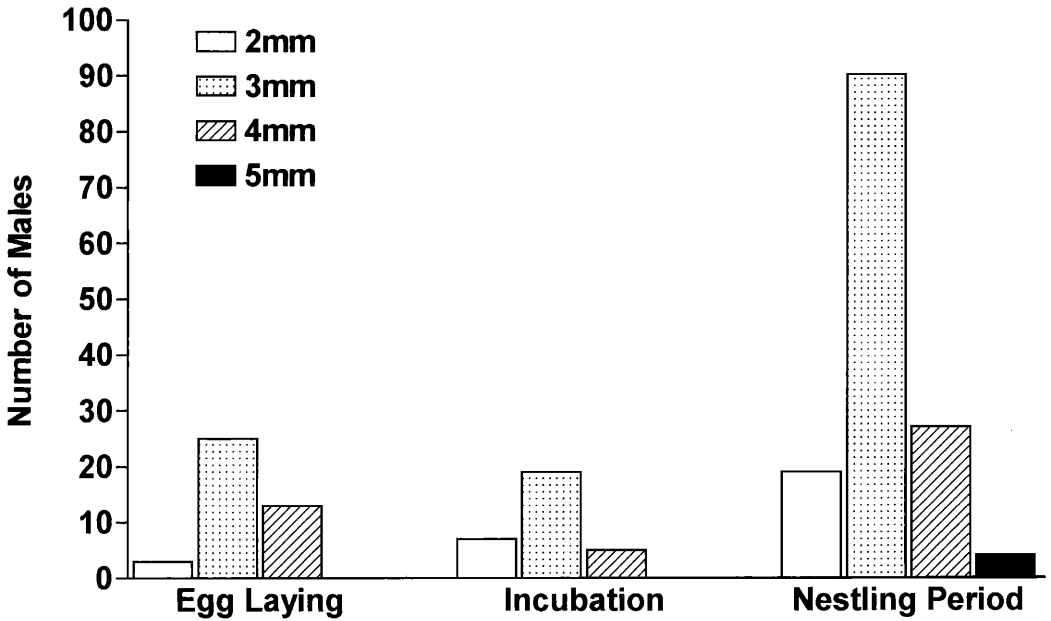


FIG. 3. Male Tree Swallow papilla length did not vary with the stage in the breeding cycle when the papilla was measured; $\chi^2 = 5.11$, $df = 4$, $P = 0.28$. Papilla length categories 4 and 5 mm were pooled in this analysis because of few males in the 5 mm category.

stage of the breeding season. Only the correlations between CP volume and right wing chord length ($P = 0.003$) during egg-laying periods and male mass ($P < 0.001$) during nestling periods remained significant after I applied sequential Bonferroni corrections for multiple comparisons (Rice 1989).

I separately analyzed data collected from males measured in multiple years to investigate possible influence of age on size of external genitalia. Initial analyses indicated that CP volume, but not papilla length, was related to the date of measurement (see above). I calculated the residuals of CP volume regressed on date to control for seasonal effects. There were no significant differences between the residuals of CP volume for males measured in two (Wilcoxon signed ranks test, $Z = -0.13$, $n = 32$, $P = 0.90$) or three (Friedman test, $\chi^2 = 0.20$, $df = 2$, $P = 0.91$) consecutive years indicating that age did not influence CP volume.

I examined relationship between CP dimensions and the Julian date of the start of egg laying and clutch size for males that were measured during their mates' egg-laying periods because that is when size of male reproductive organs had their greatest potential to directly influence male fertilization success. I analyzed the relationship between CP dimensions and papilla length and Julian date for clutch initiation separately for males mated to ASY and SY females because ASY females (mean Julian date = 135.33 ± 8.17 , $n = 202$) began egg laying earlier than did SY females (144.48 ± 9.78 , $n = 44$) ($t = 6.49$, $df = 244$, $P < 0.001$). There were no significant correlations between CP dimensions and papilla length and the Julian date for clutch initiation for males mated to ASY or SY females (all $P > 0.05$). I pooled data from males mated to ASY and SY females because in contrast to previous studies (Stutchbury and Robertson 1988), the mean clutch sizes of ASY (5.41 ± 0.95 , $n = 184$) and SY (5.11 ± 0.95 , $n = 36$) females were not significantly different ($t = -1.75$, $df = 218$, $P = 0.08$). There were no significant correlations between either CP dimensions or papilla length and clutch size (all $P > 0.05$).

Discussion.—Seasonal variation in CP size of male Tree Swallows reflected changing male reproductive opportunities over the course of the breeding season. Male CP dimensions were largest when their mates were fertile and laying eggs (Fig. 1) and early in the season (Fig. 2) when fertile extrapair females, and thus opportunities for extrapair fertilizations, were most abundant. Peer et al. (2000) observed a significant linear increase in male Tree Swallow CP volume with date during nest building and egg laying. Similarly, CP size declined in Smith's Longspur (Briskie 1993) and Bearded Tits (Sax and Hoi 1998) as the breeding season progressed. Relationship between Tree Swallow CP volume and Julian date (Fig. 2) suggests a steady decline in CP dimensions over time rather than individual facultative responses to availability of breeding opportunities (Sax and Hoi 1998).

Decrease in CP size over the course of the breeding season is consistent with the steady decrease in reproductive opportunities for male swallows. Male reproductive opportunities steadily decrease as the season progresses because Tree Swallow breeding seasons are relatively short, egg-laying within populations is fairly synchronous, second clutches are rare (Robertson et al. 1992), and clutch size decreases as the season progresses (Stutchbury and Robertson 1988). The decrease in CP dimensions over the course of the breeding season implies that the costs of maintaining a large CP is high (Sax and Hoi 1998) for Tree Swallows. That explanation is also consistent with the observation that development of male external genitalia (Sax and Hoi 1998, Peer et al. 2000) and testosterone levels (Farner and Wingfield 1980, Reyer et al. 1986) are influenced by reproductive opportunities. Papilla length in male Tree Swallows did not vary over the course of the breeding season implying that its size is not influenced by availability of reproductive opportunities.

Cloacal protuberance dimensions and papilla length were not associated with a male's age or the age class of his mate, the date she started laying eggs, or her clutch size. Thus, papilla length and CP dimensions, and by implication the size of sperm stores, alone are not predictors of an individual male's reproductive success in Tree Swallows. Kempnaers et al. (1999) found that extrapair males had larger CP volumes than did the males they cuckolded, probably because extrapair males did not deplete their sperm stores by frequent copulations. That implies that numerical advantage of sperm of extrapair males allowed them to out compete the sperm of within-pair males (Kempnaers et al. 1999). Interestingly, those extrapair males were not more successful at avoiding being cuckolded at their own nests (Kempnaers et al. 1999). Cloacal protuberance dimensions and papilla length were associated with few morphological characteristics that might indicate male quality or condition.

The CP of Tree Swallows contains the seminal glomera and functions to store spermatozoa (Peer et al. 2000). In Briskie's (1993) analysis of relationships among CP dimensions, testes size, sperm storage tubule number and length, and sperm length, Tree Swallows were more similar to some polygynandrous and polygynous bird species than they were to other monogamous birds.

It is unlikely that the CP serves as a phallus to facilitate copulation (Wolfson 1954a, 1960; Mehrotra 1982) because it is too large to insert into the female's cloaca (Birkhead et al. 1993). However, the phallus-like papilla of male Tree Swallows may function as an intromittent organ because it is small enough to insert into the cloaca. Birkhead and Hoi (1994) and Sax and Hoi (1998) argue that the Bearded Tit papilla is an intromittent organ but provide no direct evidence supporting their assertion. Although it seems likely, whether or not the papillae of Bearded Tits and Tree Swallows function as

intromittent organs awaits careful study of the anatomical mechanics of copulation in those birds.

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Observational Learning in Hummingbirds

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ABSTRACT.—Migratory hummingbirds forage on diverse assemblages of flowers varying in shape, color, and accessibility. Do hummingbirds learn to feed from flowers by observing other hummingbirds? Learning abilities of Ruby-throated (*Archilochus colubris*), Broad-tailed (*Selasphorus platycercus*), and Rufous (*S. rufus*) hummingbirds were studied in the presence or absence of a knowledgeable tutor. In two sequential trials hummingbirds learned to feed from artificial feeders of increasing complexity. Feeders in the first trial had easy access and were colored red at the nectar spout. In this initial trial, hummingbirds attempted to feed from the artificial feeder regardless of tutor presence, but tutored birds learn to feed more quickly. Feeders in the second trial were uncolored and the nectar spout was surrounded by a long artificial corolla. Tutored birds again learned to feed more quickly than their solitary counterparts. However, both untutored and tutored hummingbirds learned to feed more quickly in the second trial than the first, suggesting that the initial task of identifying a novel feeding resource is more difficult than learning how to access an identified resource.

Animals that easily learn how to use novel food resources can quickly adapt to novel environments (Greenberg 1989) and are more likely to be able to cope with urbanization (Sasvári 1979). The adoption of novel food resources is facilitated by the ability to learn through observations of animals feeding from those resources. That behavior, termed observational learning, applies to any problem-solving situation in which an animal that has viewed an experienced

demonstrator learns a behavior more quickly than an animal that has not (Davey 1981). Observational learning can lead to the rapid spread of a new foraging behavior, such as the opening of milk bottles by Tits (genus *Parus*) in Great Britain (Fisher and Hinde 1949, but see Sherry and Galef 1984, 1990).

North American migratory hummingbirds consume flower nectar from a large number of plant species across their considerable wintering and breeding ranges (Grant and Grant 1968). For example, the Rufous Hummingbird (*Selasphorus rufus*) reaches its northern range limit of southern Alaska during the summer breeding season and its southern limit of southern Mexico during the winter (Calder 1993). Throughout the range of hummingbirds, the flowers they pollinate are typically displayed according to the “hummingbird flower syndrome” (Feinsinger 1987) classified as primarily red, tubular flowers. However, North American migratory hummingbirds also feed from flowers that are neither tubular nor red (Grant and Grant 1968) including flowers with white, free-petals and unfused corollas such as *Eucalyptus* spp.

Presence of nectar in different flowers must be learned at two critical stages of a migratory hummingbird's life history: at fledging and during the first migration cycle. Fledgling hummingbirds follow their mother for several weeks after leaving the nest and eventually learn to feed from the same flowers that she does (Schuchmann 1999). The mode of floral learning by fledgling hummingbirds is not known, but observational learning is a likely candidate. After fledging, North American hummingbirds undergo considerable migrations during which time they are again forced to learn new flowers at each stage of the round-trip journey back to the breeding habitat. In addition, year-to-year variation in flower abundance will probably result in selection for learn-

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