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BEHAVIOR SUGGESTS THAT ADELAIDE'S WARBLERS (*SETOPHAGA ADELAIDAE*) ARE NOT SEXUALLY MONOGAMOUS

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Abstract: Extra-pair mating behavior has never been reported in Adelaide's Warblers (*Setophaga adelaidae*), a socially monogamous bird endemic to Puerto Rico and Vieques. However, during a study of foraging and territorial behavior in Guánica Dry Forest, I observed vocalizations and associated behaviors suggesting that extra-pair copulations occurred in 2010. Males intensely mate-guarded their females, following them at distances of one to a few meters. Both sexes were seen to make extra-territorial forays into neighbors' territories, and females stopped defending territories against intruding males when their mates were not present. I also documented seven probable extra-pair copulations, involving seven of the eight pairs monitored, plus one apparently unpaired male. These observations are consistent with the breeding synchrony hypothesis.

Key words: Adelaide's Warbler, *Setophaga adelaidae*, extra-pair mating, Puerto Rico

Resumen: EL COMPORTAMIENTO SUGIERE QUE *SETOPHAGA ADELAIDE* NO ES SEXUALMENTE MONÓGAMA. La conducta de apareamientos extra-pareja nunca ha sido registrada en *Setophaga adelaidae*, una especie socialmente monógama y endémica de Puerto Rico y Vieques. Sin embargo, durante un estudio de conducta territorial y forrajeo en el bosque seco de Guánica, observé vocalizaciones y conductas asociadas que sugieren copulaciones extra-pareja ocurridas en 2010. Los machos custodiaban fuertemente a las hembras con las que se habían apareado siguiéndolas a distancia de uno a varios metros. Ambos sexos fueron vistos realizando incursiones extraterritoriales rápidas en los territorios de sus vecinos y las hembras defendiéndolos de los machos intrusos cuando sus parejas no estaban presentes. También documenté siete posibles cópulas extra-pareja que involucraban a siete de las ocho parejas monitoreadas y un macho aparentemente sin pareja. Estas observaciones son consistentes con la hipótesis de la cría sincrónica.

Palabras clave: apareamientos extra-pareja, Puerto Rico, *Setophaga adelaidae*

Résumé : DES DONNÉES COMPORTEMENTALES SEMBLENT INDIQUER QUE LA PARULINE D'ADÉLAÏDE (*SETOPHAGA ADELAIDAE*) N'EST PAS SEXUELLEMENT MONOGAME. Les comportements d'accouplement hors couple n'ont jamais été décrits chez la Paruline d'Adélaïde (*Setophaga adelaidae*), un oiseau monogame endémique à Porto Rico et Vieques. Toutefois, au cours d'une étude sur la recherche de nourriture et le comportement territorial dans la forêt sèche de Guánica en 2010, des vocalisations et des comportements associés ont été notés, suggérant que des copulations hors couples ont eu lieu. Les mâles surveillaient de près leur partenaires, les suivant à une distance allant d'un à quelques mètres. Les deux sexes ont été vus faire des incursions dans les territoires voisins, et les femelles arrêtaient de défendre les territoires vis-à-vis des mâles intrus lorsque leurs partenaires n'étaient pas présents. Sept copulations ayant probablement eu lieu hors couple ont été décrites, impliquant sept des huit couples suivis, ainsi qu'un mâle apparemment non apparié. Ces observations concordent avec l'hypothèse de synchronisation de la reproduction.

Mots clés : Accouplement hors couple, Paruline d'Adélaïde, Porto Rico, *Setophaga adelaidae*

Extra-pair mating, which was once thought to be rare, is now recognized as common in many socially monogamous species (see reviews by Griffith *et al.* 2002, Westneat and Stewart 2003). This is mostly due to an increase in the number of studies that look at genetic parentage, which have demonstrated extra-pair fertilizations in species where direct observation of extra-pair copulation is difficult. While genetic studies of extra-pair mating have burgeoned in recent years, behavioral research has been limited to relatively few, often well-studied, species. Most behavioral research has occurred in temperate species.

Several behaviors are indicative of extra-pair mating tactics. Mate guarding, the close following of mates to ward off extra-pair solicitations or attempted extra-pair copulations, is often associated with extra-pair mating. Although mate guarding does not guarantee that a male will not be cuckolded, especially if females actively seek extra-pair copulations (Sheldon 1994, Kempenaers *et al.* 1995, Johnsen *et al.* 1998), it can be an effective strategy (Chuang-Dobbs *et al.* 2001). Stronger evidence is provided by extra-territorial forays, although forays can also arise as a result of individuals foraging in higher quality territories or as a result of conspecific brood

parasitism. In migratory species, it has also been suggested that females may use extra-territorial forays to assess the quality of neighboring males (Chiver *et al.* 2008). However, resident species have an opportunity to assess the quality of neighbors during territorial battles and other interactions during the non-breeding season (Smith 1988, Otter *et al.* 1994), and may not need to further assess the quality of potential extra-pair mates during the breeding season.

Several hypotheses have examined conditions that are associated with extra-pair mating. Increased population density has been hypothesized to increase access to extra-pair mates and increase rates of extra-pair mating. However, the few studies conducted have found population density to be relatively unimportant (Tarof *et al.* 1998, Stutchbury and Morton 2001). Vegetation structure is also hypothesized to affect rates of extra-pair mating, by affecting the ability of individuals to guard their mates against intruders. Indeed, two studies have found that extra-pair mating is more likely to occur in densely vegetated areas (Mays and Ritchison 2004, Tryjanowski *et al.* 2007). Increased synchrony in breeding populations may also increase rates of extra-pair copulations, since it allows females to more easily assess male quality and makes it worthwhile for males to compete for extra-pair copulations (the Breeding Synchrony hypothesis; Stutchbury and Morton 1995, Stutchbury and Neudorf 1998).

Adelaide's Warbler (*Setophaga adelaidae*) is endemic to the sub-tropical islands of Puerto Rico and Vieques. Like many resident tropical species, pairs defend a multi-purpose territory year-round (Toms 2010), and males provide parental care (Spaulding 1937, Staicer 1991). However, the timing of the breeding season depends on rainfall patterns, usually being limited from March to June (Toms 2010), a breeding season more typical of temperate species. Adelaide's Warblers are thought to be strictly socially monogamous (Staicer 1991), and copulatory behavior has been seen previously only in established pairs (Staicer 1996b). However, during a study of foraging and territorial behavior in Adelaide's Warblers, I observed behavior suggesting that extra-pair copulations occur in at least one population of this species.

METHODS

Observations were made in the Guánica Dry Forest (a commonwealth forest and an international biosphere reserve) in southwest Puerto Rico. The Guánica Dry Forest is a seasonally dry forest, with upland areas characterized by semi-deciduous scrub forest. In the two focal areas surveyed in this study, typical tree heights were < 5 m, with occasional larger emergent trees at suitable microsites. The understory was extremely dense in some locations, but was more commonly a mixture of shrubs and small trees. Visibility rarely exceeded 10–15 m at eye level.

Behavioral observations reported here were opportunistically noted during an ongoing study of territorial and foraging behavior of a single population of Adelaide's Warblers, assessed independently during the winter and spring of every year from 2006–2010. Individual Adelaide's Warblers were previously captured in mist-nets and marked with unique color-band combinations. Individuals were sexed using plumage characteristics (Fig. 1) and behavior, and aged using plumage characteristics. All banded individuals were at least 2 yr old at the time of this study. I was unable to capture some individuals for color-banding, but all pairs observed had at least one individual marked.

Territorial and foraging behaviors were observed by following focal individuals through the forest, on grids marked at 15 m intervals. Total observation time per individual varied, but mean observation time was 1 hr 55 min. Only a single individual was observed for less than 1.5 hr during the breeding season. All individuals included in this study had been observed for a minimum of three observation intervals previously, including the preceding non-breeding season (21 February to 22 March 2010), and were habituated to my presence, approaching to within 1 m of me. Observations reported here were obtained from 30 May to 6 June 2010 on eight pairs and one apparently unpaired male. All pairs observed had well-established pair-bonds at least 2 mo prior to these observations, and many had been paired for several yr (pers. obs.). In addition, all pairs used song-response duets typical of established pairs (Staicer 1996b).

No nest searching was conducted, so the timing of these behaviors relative to the nesting cycle cannot be confirmed. However, the behavior of females and occasional sighting of females carrying nesting material strongly suggests that these observations were made during the period of nest-building and egg-laying. Breeding synchrony seemed to be very high in 2010, possibly due to the sudden onset of heavier rains in May, after a long period of dry weather. Breeding behavior was not recorded systematically, and instances of extra-pair mating be-

Fig. 1. Male Adelaide's Warblers (left) have thicker and longer black eyestripes and more black flecking in the crown than females (right). Both photos are of adults. Additional criteria for distinguishing among age and sex classes can be found in Toms (2011). Photos by Judith Toms at the Guánica Dry Forest, Puerto Rico, on 10 March (male) and 10 January 2009 (female).

haviors could have gone undetected in previous years.

RESULTS

FORAGING AND TERRITORIAL BEHAVIOR

During early June 2010, females appeared to spend more time foraging near the edges of their territories than they had during the non-breeding season. Females also seemed to "pip" more frequently while foraging than during the non-breeding season (see Staicer 1991 for a description of the pip call) even though their mate was almost always nearby. Males rarely foraged apart from their mate during the breeding season (see Mate Guarding Behavior below), even though pairs often separated widely during the non-breeding season.

During the breeding season, fights were most commonly observed in territories where females were being mate guarded; fights were rare in territories where females appeared to be incubating. Many fights involved neighboring males that were outside of their previously established territorial boundaries (see Extra-territorial Forays section below). Females were not observed defending against intruding males when alone, although they occasionally joined in territorial battles along with their mate. This differed from their behavior during the non-breeding season, when individuals of both sexes defended their territory against intruders of either sex.

MATE-GUARDING BEHAVIOR

During the non-breeding season, established Adelaide's Warbler pairs typically forage independently, maintaining vocal contact but spending extended periods of time without visual contact (Staicer 1996b, pers. obs.). In contrast, during the breeding season males spent most of their time following their mate at distances of 1 to a few m. However, they did occasionally separate from her to sing from song perches near their territory boundary or to fight with neighbors.

Males often appeared agitated while mate guarding, looking around frequently and sometimes using a moderately aggressive posture, where the tail was cocked upwards, and the wings were held or flicked down and out (Staicer 1991, Toms 2010). Two males appeared to be particularly agitated following several extra-territorial forays into their territories by neighbors, and guarded their mates more closely thereafter. One also increased the intensity and duration of his aggressive postures.

EXTRA-TERRITORIAL FORAYS

Extra-territorial forays into neighboring territories

were rarely seen during the non-breeding season, but were frequently observed during the breeding season. Extra-territorial forays, all into adjacent territories, were seen by several males. Most extra-territorial forays involved an apparently unpaired color-banded male, who was frequently seen flying into or out of two neighboring territories, and who sang almost entirely on the borders of these territories. I once observed this male more than 40 m into one of his neighbors' territories, nearly at the territory midpoint. His extra-territorial forays lasted for one to several minutes, and often ended in a fight with the neighboring male.

An extra-territorial foray was also confirmed for one female. Immediately after a song from a neighboring male, she made a brief (≈1 min) foray into his territory, to roughly the same location where he had just sung. At this time, her mate was occupied in fighting an intruder in another part of their territory.

APPARENT EXTRA-PAIR COPULATIONS

I detected seven probable extra-pair copulations during these 7 days of observations. Probable extra-pair copulations were most common during 0645–0845 (1-3 hr after sunrise; $n = 6$), but also occurred once in the late morning (1055). I deemed that an extra-pair copulation had likely occurred if I detected distinctive behaviors associated with copulation: female Adelaide's Warblers rapidly flutter their wings and both sexes trill or twitter during copulations (Staicer 1991). This trill or twitter differs from other Adelaide's Warbler vocalizations reported (Staicer 1991), and I never heard such vocalizations during the non-breeding season, or when birds were alone. The wing fluttering also produces a distinctive sound that I did not detect during the non-breeding season. Unfortunately, I was unable to visually confirm that copulation had actually occurred, because Adelaide's Warbler copulations are brief, lasting only a few seconds (pers. obs.), and usually obscured by vegetation. Interestingly, although another vocalization, copulation songs, are always used by the male during within-pair copulations (Staicer 1991), they were not always used during the extra-pair copulations observed.

In only one instance was I able to confirm that the individuals were not paired. This probable copulation involved an unbanded female and a color-banded male, who was paired with a color-banded female. In four instances, I was able to visually confirm the identity of one of the individuals and was fairly certain of the identity of the other individual, based on their movement towards their territory. In the sixth instance, I was fairly certain of the identity of the male, as I followed his songs from well within his territory, into another territory where a probable copulation occurred, and back into his territory. Unfortunately, he was moving too quickly for me to confirm his identity and he did not sing immediately after returning to his territory. In the last instance, I was able to confirm that the probable copulation had involved two unbanded individuals, and followed the male back into a known territory that was held by a banded female and an unbanded male.

DISCUSSION

Extra-pair copulations have not been reported previously for Adelaide's Warbler. Although I could not visually confirm any extra-pair copulations in this study, probable extra-pair copulations were detected in all but one of the pairs under study. Males guarded their mates intensely during a period when extra-pair copulations could occur, spending the majority of their time following their mate at distances of 1 to a few m, and using moderately aggressive postures. This strongly differs from their behavior during the non-breeding season, when paired individuals often forage at distances of tens of m apart, maintaining only vocal contact (pers. obs.). Mate guarding has not been reported previously in this species, although mate following is known to occur when pairs are becoming established (Staicer 1996b).

Female behavior suggests that they are willing participants in extra-pair copulations. Females did not defend against neighboring males making forays into her territory during the breeding season unless their mate was present, even though they vigorously defended their territory against all intruders during the non-breeding season. Breeding females also pipped frequently when foraging near the edges of their territories. Although the pip calls could be used for communication within a pair, they seem unnecessary for that purpose when the male is in such close proximity, and could serve to ensure that neighboring males know where she is. Rate and type of female vocalizations are known to provide information about fertility and location in other species (Montgomerie and Thornhill 1989, Neudorf *et al.* 2008, Hung *et al.* 2009), and may be used to directly solicit extra-pair copulations (Sheldon 1994, Tarof and Ratcliffe 2000, Tarof *et al.* 2005).

Both sexes were seen to make forays into neighboring territories. These intrusions were typically silent and of relatively short duration, similar to

those seen in Hooded Warblers (*Setophaga citrina*; Neudorf *et al.* 1997, Stutchbury 1998). It is unlikely that extra-territorial forays are primarily for the purpose of foraging in higher quality territories, since arthropods are available in much greater quantities during the breeding season than in late winter, and extra-territorial forays were not seen during times of food shortages (J. D. Toms unpubl. data). Similarly, conspecific brood parasitism is unlikely because the one documented extra-territorial foray by a female took place several hr after sunrise, and it is likely that Adelaide's Warblers lay eggs near dawn as seen in their congeners (McMaster *et al*. 1999, 2004). Thus, the primary reason for extra-territorial forays in this species would seem to be extra-pair copulations.

It is not clear why extra-pair copulations were not seen or suspected in a previous study of breeding behavior of Adelaide's Warblers at Cabo Rojo Wildlife Refuge (Staicer 1991). It is possible that extra-pair copulations did occur, but were not observed due to the briefness of these encounters. However, Staicer (1991) worked in a more open, savannah-like habitat, and emphasized vocalizations, which should have increased the likelihood of observing behavior suggestive of extra-pair copulation. A more likely possibility is that extra-pair copulations are more common in Guánica Dry Forest, at least in some years. The denseness of the Guánica Dry Forest may make it more difficult for males to defend against intruders from song perches, as they might do in Cabo Rojo. This could result in both a greater need for mate-guarding, and a greater likelihood that extra-territorial forays will result in successful extra-pair copulations.

Differences in breeding synchrony could also affect mating systems between these two sites. Indeed, breeding synchrony appeared to be high in Guánica in 2010, when extra-pair copulations were frequent, and low in Cabo Rojo where no extra-pair copulations were seen (Staicer 1991). Moreover, little extra-pair mating behavior was seen in Guánica in 2009, when the breeding season was relatively asynchronous (J. D. Toms unpubl. data). Although the breeding synchrony hypothesis does seem to explain observed differences in extra-pair mating in this species, caution is required as two key assumptions of the hypothesis may not have been met. First, males do not seem able to seek extra-pair copulations without affecting their ability to effectively mate-guard: the one extra-territorial foray by a female occurred while her mate was fighting an intruder instead of following her. Second, female Adelaide's Warblers should be able to effectively assess male quality throughout the non-breeding season, when territorial displays and fights occur on a daily basis (Toms 2010). The only breeding-season-specific cue that females do not have available during the non-breeding season is the Type B song, which is used exclusively for close-range aggression among males (Type A songs are used for mate attraction; Staicer 1996a). It is possible that extra-pair mating behavior does occur in Adelaide's Warblers when breeding is relatively asynchronous, but is more difficult to observe because fewer individuals are participating or individuals participate at a lower rate.

In conclusion, while I was unable to visually confirm any extra-pair copulations in this short study, the high proportion of pairs in which probable extra-pair copulations were noted strongly suggests that extra-pair copulations do occur in this population, at least when circumstances promote synchronized breeding. Given the difficulty of observing any copulation in this habitat, either within-pair or extra-pair, genetic confirmation of parentage is probably the most efficient method to confirm that extra-pair copulations do occur in this species, and establish its frequency. Adelaide's Warblers may be a good species to test the mechanisms underlying extra-pair mating systems, as significant differences may occur among populations, and even among years in the same population.

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