

TERRITORY ACQUISITION BY ISLAND SCRUB-JAYS: HOW TO BECOME A BREEDER

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Abstract—The island scrub-jay (*Aphelocoma insularis*) is an endemic resident of Santa Cruz Island. Earlier studies have shown these birds to be permanently territorial and monogamous. Young birds generally take three or four years to obtain a territory. The most common method is for a pre-breeder to replace a member of an established pair of like sex upon its death. Other documented methods include a new pair usurping a territory upon the death of one breeder, and establishment *de novo* between established breeders. Territorial changes among older breeders can also occur by fusion of adjacent territories, and divorce followed by re-pairing. Whatever the strategy used, obtaining a territory and being part of a territorial pair is prerequisite to becoming part of the breeding population.

Keywords: *Aphelocoma insularis*, behavior, island scrub-jay, Santa Cruz Island, and territory acquisition

INTRODUCTION

Jays of the genus *Aphelocoma* have been the subject of many studies dealing with their distribution (Pitelka 1951), mating systems (Woolfenden and Fitzpatrick 1984, Carmen 1988, Burt and Peterson 1993), demography and survival (Fitzpatrick et al. 1986, Atwood et al. 1990), and evolutionary history (Peterson 1992, Peterson and Burt 1992, Rice et al. 2003). Endemic to Santa Cruz Island, the island scrub-jay (*Aphelocoma insularis*) is among the most distinctive of these jays and certainly the most strongly differentiated element of the California Channel Islands avifauna (Pitelka 1951, Johnson 1972).

Since 1975, the island scrub-jay has been the focus of a continuing study that has, to date, provided data on its breeding biology and social system (Atwood 1980a, 1980b), survival and demography (Atwood et al. 1990, Corey 1994, Collins and Corey 1994), territory size and island-wide population size (Kelsey 1998, Kelsey and Collins 2000), as well as seasonal weight variation (Atwood 1980c) and skeletal morphology (Isitt 1989). These studies have shown that island scrub-jays are monogamous, occurring in permanently territorial pairs and lack the distinctive cooperative breeding system of the congeneric Florida scrub-

jay (*A. coerulescens*) (Woolfenden and Fitzpatrick 1984), and one population of the western scrub-jay (*A. californica*) in Oaxaca, Mexico (Burt and Peterson 1993). Young jays disperse from the parental territory shortly after fledging and wander independently until acquiring a suitable territory; some die without ever obtaining a territory. First breeding is typically at the age of 3–4 years (Collins and Corey 1994, Corey 1994). This pivotal transition from wandering pre-breeder to territory holding reproductive adult is the subject of this analysis.

METHODS

In this study we monitored a population of island scrub-jays in the Central Valley of Santa Cruz Island, primarily within a one mile radius of the Channel Islands Field Station of the University of California Natural Reserve System. When captured, the jays are banded with a U.S. Fish and Wildlife Service numbered aluminum band and a unique combination of three or four colored acetate bands, making each bird individually identifiable by sight. This study began in 1975 when 10 pairs were followed to determine their mating system and biology (Atwood 1980a, 1980b). Since 1994,

the study population has consisted of approximately 80 breeding pairs and an unknown number of pre-breeding young birds. A complete census is conducted twice a year, in the spring and fall, during which the status of all breeding pairs in the study area is checked and all other color-banded individuals, mostly wandering pre-breeders, are recorded. In addition, two to four trips to the study area are made annually, in both spring and fall, during which new birds are captured and banded and some older birds are recaptured for replacement of worn or broken color bands. All color banded jays observed on these trips are also recorded. The age at first capture is determined by plumage characters (Pitelka 1945) which allow young jays (<12–14 months old) prior to the end of their first complete prebasic molt to be separated from older or adult birds. Sex can be estimated by size and weight of the jays when captured and is later confirmed by the distinctive burr or “rattle” vocalization only given by territory-holding females (Atwood 1980a, Curry and Delaney 2002). Jays were considered to be a pair when found defending a territory against intruders on two or more consecutive censuses and by observing their responses to each other’s actions and vocalizations. The low divorce rate documented herein reinforces our view that the young birds we have considered wandering pre-breeders have not bred nearby prior to obtaining a territory on the study plot. Territory-holding individuals which were not located on two sequential seasonal censuses were assumed to have died. In fewer than five cases a jay which was absent, and presumed dead, was found alive nearby at a later date; none were ever found outside the study area. In almost all cases the cause of death was not determined. Banding was carried out under master bird banding permit 08707 issued to Collins and protocols 154 from the Animal Welfare Board, California State University and 570 from the Animal Care and Use Committee, University of California, Santa Barbara, were followed.

RESULTS

Our annual censuses of between 10–89 pairs (1,267 pair-years), made over nearly three decades, showed that 72.0% of the pairs remained together

from one spring census to the next, leaving few opportunities for territory seekers. Pre-breeding island scrub-jays acquired a breeding territory by one of several means, including: (1) replacement of a breeder of either sex, (2) usurping of a territory by two pre-breeders upon the death of one breeder and, (3) *de novo* formation of a territory between existing territories. Established breeders also acquired new territory by fusion of adjacent territories and through divorce and re-pairing. Some of these strategies were regularly recorded and others are decidedly uncommon occurrences.

By far the most common method for a pre-breeder to acquire a territory was to replace a missing and presumed dead breeder. Of the 354 pair changes we observed, 105 (29.8%) involved males replacing missing males and 130 (36.7%) were of females replacing missing females. The surviving member of the original pair and the replacement male or female continued to defend the original territory with little apparent change in its size or location. We have no direct observations of this process and cannot comment on how long it takes for the missing breeder to be replaced, however, we believe it to be rapid. In the spring, would-be replacement females were seen on territories when the resident female was on the nest incubating and only seemingly absent. These intruder females quickly leave when the resident female reappears. This suggests that pre-breeders are carefully monitoring breeding pairs and are quick to take advantage of any opportunity to replace a missing breeder.

On 91 (25.7%) of all pair changes, both members of a breeding pair disappeared between consecutive annual spring censuses, and in such cases a new pair had often established itself in the previously occupied territory. The exact sequence of events leading to this dual replacement is not always clear. It is possible that one member of the original pair died and was replaced by a prospecting pre-breeder. Then, shortly thereafter, the remaining member of the original pair was similarly lost and also replaced by a pre-breeder resulting in the new pair being present on the original territory. However, in six cases (1.7%) one member of the original pair was located elsewhere. It appeared to have been unable to acquire a new mate fast enough to aid in territory defense and prevent its being ejected from its territory. This

supports the conclusion that, in at least some cases, following the death of one individual a replacement pair took over the territory and succeeded in ejecting the surviving member of the original pair. In one well documented case a new pair took over the majority of a widowed male's territory. He continued to hold only a peripheral portion of his former territory before subsequently moving to a nearby area where he established a new territory and obtained a new mate. Ejections were not limited to one sex, as we have documented four cases of males and two cases of females being ejected. In two cases, both involving males, the ejected bird established a nearby territory with a new mate within a year. One ejected female replaced a missing female on a nearby territory, but only after being an unpaired wanderer for three years. We also documented two ejected males and one ejected female remaining unpaired non-breeders for up to a year before disappearing permanently. An anecdotal observation of a male and female attempting to invade an established territory together, suggests that pre-breeders may establish a pair bond. This could enhance their ability to gain reproductive status by together taking over a breeding territory and ejecting a widowed survivor.

Territory boundaries often shift slightly from year-to-year (Kelsey 1998), therefore it is possible for a territory to be formed *de novo* between previously existing territories. We cannot differentiate between the territory being formed by a paired duo of pre-breeders or a single male who subsequently attracted a mate once the new territory had been established. However, in two instances single pre-breeding males were observed exhibiting territorial behavior on a less well-defended border of an established territory. Their activities seemed rather secretive and their territorial vocalizations muted. In neither case were they able to maintain the new territory for more than a few days. We have only documented two cases (<1%) of *de novo* territory formation within the core of our study area. New pairs are frequently encountered on the periphery of our study area, but it is not known if these are pairs on newly formed territories or established pairs whose territory boundaries have shifted and now abut those of the study population.

On 12 occasions (3.3% of all pair changes) we have documented fusion of adjacent territories following the death of a male and a female of the two neighboring pairs. Again, in these situations only the end result and not the exact sequence of events was observed. In each instance we found a male and a female from two previously adjacent pairs mated and inhabiting parts of the two original territories. In one case, where more details were known, the fusion resulted in the ejection rather than the death of one of the original pair members. In this case, the male of a long established pair (Pair 1) died and was replaced by a young pre-breeder male. Less than a year later, the female from the similarly long-established pair on the adjacent territory (Pair 2) also died. During the next spring census we found a fusion of the two territories with the female of Pair 1 now mated with the male of Pair 2 and defending a new territory consisting of parts of each of the two original territories. The younger replacement male from Pair 1 was found alive on a new territory located about 4–5 territories away with a new female mate. It is possible that the older male of Pair 2, upon the death of his mate, ejected the younger male of Pair 1 and paired with his older female mate. It is equally possible that the female of Pair 1 divorced her younger less experienced mate in favor of the older established male of Pair 2. In another less well documented case we strongly suspect that an older female did divorce and abandon a less experienced replacement mate; her new mate was not identified. Her abandoned mate soon attracted a new female and held the original territory for several years.

We documented only seven cases (2.0% of all pair changes) of divorce and re-pairing among the island scrub-jays. In these instances both members of established pairs were subsequently found alive but paired with different mates in subsequent breeding seasons. Again, the exact sequence of events is not known and we have no data on their reproductive success before or after the divorce which might explain this behavior.

DISCUSSION

Replacing a missing breeder or taking over a territory are clearly important strategies for young

island scrub-jays to become reproductive adults. The rapidity of replacement and general stability of territory locations from year-to-year (Kelsey 1998), suggest that breeding territory habitat is saturated and opportunities to become a breeder are at a premium. This is consistent with the well documented delayed reproduction of young island scrub-jays (Corey 1994, Collins and Corey 1994). Replacement of deceased breeders by pre-breeding floaters is the most common mode of obtaining breeding status and territory among *Aphelocoma* jays (Woolfenden and Fitzpatrick 1984, 1990, 1996, Carmen 1988, 2004) and perhaps most permanently resident passerine birds. Such replacement is often rapid, sometimes within one day (Desrochers et al. 1988). Partnerships of two or more same-sex individuals have been shown to be competitively superior to single individuals in obtaining a breeding territory in several cooperative breeding species (Ligon and Ligon 1979, 1982, Koenig 1981, Koenig and Mumme 1987). Opposite sex pairing of young passerines prior to the onset of breeding is much less common although it has been recorded for several species of chickadees and tits (Paridae; Smith 1984, 1991) and California Gnatcatchers (Atwood and Bontrager 2001). It occurs in <5% of prebreeding western scrub-jays (Carmen 2004).

Fusion of territories and divorce followed by repairing do not represent initial acquisitions of territories or mates, but rather a change in territory boundaries and acquisition of a new mate. The few examples of these we have documented to date (3.3% and 2.0% respectively) allow only limited speculation regarding the possible value, in terms of increased future reproduction, of obtaining an older more experienced mate as opposed to a younger and less experienced mate. However, in a long-lived species as the island scrub-jay (Atwood et al. 1990), obtaining a more experienced mate may, in the long run, be the more successful strategy. The fusion of adjacent territories is not unique to island scrub-jays and has been documented previously for Florida scrub-jays (Woolfenden and Fitzpatrick 1984, 1990, 1996) and the black-capped chickadee (*Poecile atricapilla* Smith 1991) among others. Similarly, divorce among otherwise permanently paired birds has also been observed in a number of species but generally at rates less than 10% (Woolfenden and Fitzpatrick 1984, 1990).

As indicated, the most common route to becoming a territory holding breeder in both Florida (48%) and island scrub-jays (66.5%), is by replacing a lost breeder. However, the absence of cooperative breeding in the island scrub-jay accounts for the major differences in the modes of territory acquisition among these congeners. Territorial budding and inheritance of part or all of their natal territory are common routes to territoriality (38% and 10% respectively) for male Florida scrub-jays (Woolfenden and Fitzpatrick 1978, 1990). Both of these modes are closely associated with cooperative breeding and thus precluded for island scrub-jays. The establishment of a territory *de novo* between existing territories has been documented in all three scrub-jay species. In the Florida scrub-jay, there is substantial year-to-year variation in family size which in turn regulates territory size (Woolfenden and Fitzpatrick 1984, 1996). These changes in territory size may well open more opportunities for *de novo* territory formation in these jays where it accounts for 4% of all territory acquisitions (Woolfenden and Fitzpatrick 1990, 1996). More stable size and configuration of territories (Kelsey 1998) may account for *de novo* territory acquisition being much less common (<1%) in the island scrub-jay. It only occurs "rarely" in western scrub-jays (Carmen 2004).

Regardless of the above strategies are used, obtaining a territory and being part of a territorial pair is a prerequisite for island scrub-jays becoming part of the breeding population. As such, it is a vital component to their overall breeding biology and shall command attention in continuing studies.

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