Animal Behaviour 84 (2012) 251–259

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Disentangling site and mate fidelity in a monogamous population under strong nest site competition

Mei-Ling Bai, Lucia Liu Severinghaus*

Biodiversity Research Center, Academia Sinica, Taipei, Taiwan

ARTICLE INFO

Article history:
Received 27 November 2011
Initial acceptance 12 January 2012
Final acceptance 19 April 2012
Available online 6 June 2012
MS. number: 11-00948R

Keywords:
better option hypothesis
decision rule
habitat-mediated mate choice
incompatibility hypothesis
Lanyu scops owl
mate fidelity
Otus elegans botelensis
path analysis
prior residence
site fidelity

Site and mate fidelity are important aspects of animal mating systems and have implications for animal population structures. In birds, they are often related to the age, breeding experience, prior residence, pair duration or breeding performance of individuals. These variables are often correlated, and site and mate fidelity may also be associated with each other. Most previous studies focused on either site fidelity or mate fidelity, and the relationship between them remains to be explored. In this study, we used path analysis to examine the correlates of site and mate fidelity of Lanyu scops owls, *Otus elegans botelensis*, and to investigate the relationship between site and mate fidelity. Site fidelity of female owls was related to previous breeding success, following a 'win-stay, lose-switch' model. Site fidelity of male owls increased with both previous breeding success and years of prior residence. Mate fidelity was related to female site fidelity and pair duration. Although mate fidelity was higher after successful breeding attempts, it was a result of the breeding success-dependent site fidelity of the owls. Many studies used the positive correlation between previous breeding success and mate fidelity to support the better option hypothesis or the incompatibility hypothesis of divorce. Our study identified the most likely causal pathway for the complex site and mate fidelity pattern in the Lanyu scops owl, and demonstrated that it is important to identify the underlying driving forces to avoid erroneous conclusions.

Site and mate fidelity are important aspects of animal habitat choice and mating systems, and have implications for animal population structures (Bateson 1983; Freemark et al. 1995; Berec & Boukal 2004). They are driven by diverse selection forces reflecting different local constraints on resources, time and energy. Site fidelity is advantageous because it removes the need to search for a new breeding site each year when suitable sites are widely scattered and costly to locate, or when competition for available sites is strong. Site fidelity also provides benefits in predator escape, territory defence and foraging efficiency because it increases familiarity with the environment (Haley 1994; Woodard & Murphy 1999; Forstmeier 2002; Morrison et al. 2008). Mate fidelity is advantageous because it removes the need to search for new mates or because reproductive success increases with pairing duration (Ens et al. 1996; Black 2001).

Birds, despite their mobility and ability to explore suitable habitats and visit potential mates, frequently settle at the same site or pair with the same mate from year to year (e.g. Fairweather & Coulson 1995; Heg et al. 2003; Hoover 2003; Berkunsky & Reboreda 2009). Their site and mate fidelity are often related to their sex, age, breeding experience, prior residence, pair duration or breeding performance (e.g. Harris et al. 1987; Badyaev & Faust 1996; Schjørring et al. 2000; Hoover 2003). Male birds usually have higher site fidelity than females (Payne & Payne 1993; Schjørring et al. 2000), presumably because males benefit more from being site faithful, as they are usually the ones responsible for establishing and defending territories. Both site and mate fidelity may increase with age or breeding experience in birds (Payne & Payne 1993; Badyaev & Faust 1996; Pyle et al. 2001). Older birds or birds that have bred for more years are usually socially dominant and are of higher quality than younger or less experienced ones, giving them a greater chance of retaining their chosen sites and mates. Site fidelity may increase with years of prior residence (the number of previous breeding attempts at a site), as the advantage associated with familiarity then also increases (Morrison et al. 2008). Similarly, a pair with longer pair duration (the number of previous breeding attempts between a pair) are often more likely to reunite, as pair coordination improves (Harris et al. 1987; Ens et al. 1996; Black 2001).

Despite the advantages associated with site and mate fidelity, dispersal or divorce may happen if the quality of the current site or

* Correspondence: L. L. Severinghaus, Biodiversity Research Center, Academia Sinica, 128 Academia Road, Section 2, Nankang, Taipei 115, Taiwan.
E-mail address: zobbowl@gate.sinica.edu.tw (L. L. Severinghaus).

0003-3472/$38.00
doi:10.1016/j.anbehav.2012.05.004

mate is low, and the expected benefits of breeding at a new site or pairing with a new mate are greater than the costs of change. Individuals often follow a 'win-stay, lose-switch (WSLS)' model, staying at the same site if the previous breeding success was high and dispersing otherwise (Switzer 1993; Lindberg & Sedinger 1997; Hoover 2003). Pairs are more likely to remain together after successful breeding attempts than after breeding failures (Dubois & Cezilly 2002; Rogers & Knight 2006).

However, age, breeding experience, years of prior residence, pair duration and breeding performance are often confounded. Because breeding success of birds usually increases with age and breeding experience (Newton 1989; Woodard & Murphy 1999), the positive association between site fidelity and age or breeding experience may arise as a by-product of the WSLS model. Pair duration is usually longer when both partners are more experienced breeders (Hall 1999; Naves et al. 2007). High mate fidelity may thus result from the preference for experienced breeders rather than for familiar partners. Few previous studies have attempted to clarify these confounding effects (e.g. Pyle et al. 2001; Naves et al. 2007). Furthermore, although high association between site and mate fidelity is found in many species (Desrochers & Magrath 1996; Cezilly et al. 2000; Setiawan et al. 2005; Naves et al. 2007), most previous studies focused on either site or mate fidelity. Divorce may be the side-effect of a change in breeding site, but empirical data are few (e.g. Desrochers & Magrath 1996; Llambias et al. 2008), and a solid analysis tool is lacking. The exact nature of the relationship between site and mate fidelity remains to be explored.

We studied the site and mate fidelity of the insectivorous Lanyu scops owl, *Otus elegans botelensis*, on a subtropical island. We applied path analysis to decompose the confounding correlates of their site and mate fidelity, as well as to investigate the relationship between site and mate fidelity. The owl breeds in natural tree cavities and the availability of suitable cavities limits the number of breeding pairs (Severinghaus 2007). Competition for nest cavities is strong. Male owls claim territories months before the onset of breeding. From prior to egg laying to the first week after egg hatching, a male provisions his mate and then his whole family. The pair bond is not maintained outside the breeding season. With a long-term data set, we investigated the following aspects of mate and site fidelity.

(1) The correlates of site fidelity. (a) As the qualities of tree cavities are highly variable but the quality of a specific cavity is relatively stable and can be predicted by previous breeding success (Severinghaus 2007), we predicted that the site fidelity of the owl would follow the WSLS model. (b) Age, breeding experience and years of prior residence can be indicators of the competitive ability of males. Given the very high nest site competition, we predicted that these indicators would correlate positively with site fidelity in males, but the correlation would be weaker in females.

(2) The correlates of mate fidelity. As provisioning by male owls is crucial to breeding success, we predicted that mate fidelity would be (a) higher in more experienced males than in younger ones, and (b) higher in pairs that had bred successfully before than in pairs that failed.

(3) The relationships between site and mate fidelity. Because of the strong nest cavity competition, a male owl is likely to occupy the nest cavity that it can best defend, while a female should choose the best nest cavity available. Therefore we predicted that the site choice of females would determine the reunion or divorce of the pairs.

(4) The longitudinal effects of site and mate fidelity. (a) Defending a familiar territory may be easier than establishing a new one and allow more energy to be allotted to reproduction. We predicted that a male breeding in the same nest cavity for a second year would have higher reproductive output than in the first year. (b) As pair coordination may improve with time, we predicted that a reunited pair would have higher reproductive output in their second year than in their first one.

METHODS

Study Site and Species

We studied Lanyu scops owls between 1985 and 2009 on Lanyu (22.0°N, 121.3°E), which is a 46 km^2 island 60 km off the southeastern coast of Taiwan. The volcanic landscape of Lanyu is covered by subtropical forests, shrubs, grasslands and agricultural fields. Our study site is an oblong patch of mature forest about 10 ha in area, on the southeastern side of Lanyu. It is a habitat island with grassy fields to the southeast and scrubby bushes to the northwest, and is dominated by Taitung longan, *Pometia pinnata*, breadfruit tree, *Artocarpus communis*, and poisonous woodnettle, *Dendrocnide meyeniana*. Lanyu scops owls breed in tree cavities. All tree cavities on Lanyu are formed through natural decay, as there are no cavity-excavating species on the island. In the study site, we mapped all the trees larger than 18 cm in diameter at 130 cm above ground, and measured the characteristics of all the cavities known (258 cavities on 119 trees among 296 trees in total; Severinghaus 2007).

The monogamous Lanyu scops owl forms pairs only during the breeding season. They are capable of breeding in their second year of life but most start breeding at 3 years or older. No Lanyu scops owl is known to move in or out of Lanyu, although most owls leave the study site (their breeding site) to winter elsewhere on the island (Severinghaus 2002; Bai et al. 2012). They return to our study site in spring, asynchronously, and reach very high densities (average of 111 ± 9 adults in 10 ha area in May). Only about 64% of them may breed owing to the shortage of suitable cavities (Severinghaus 2007). Extrapair copulation is frequent in the early breeding season, but extrapair fertilization is extremely rare (Hsu et al. 2006). Male owls claim territories through intensive vocal contests in March and April. Territory owners defend only the immediate vicinity of the nest cavity, although this insectivorous owl has large activity areas (average daily activity area in March: 4.9 ± 2.5 ha) and forages in both forest and grassy field (Severinghaus 2001a). Egg laying takes place mainly in May. Females lay one to three eggs and incubate alone for about 1 month (Severinghaus 1992). Males provision their mates and young while females stay in the nest cavities to incubate and brood the nestlings until the nestlings are 7–10 days old, then females also participate in feeding the young. Young owls fledge at around 30 days, and are further fed by both parents near the nest cavities for about 1 month (Severinghaus 1992, 2001b). The annual survival rate of adult owls is 0.75 (Severinghaus & Rothery 2001).

Field Work

Between 1985 and 2009, we captured adult owls with mist nets and nestlings from nest cavities at about 3 weeks of age. Since 1999, about 80% of the population has been individually colour-banded for identification, of which about one-third were banded as nestlings. We identified the sex of adults by their sex-specific vocalizations and breeding behaviour. After 1999, we collected about 20 μl of blood from the alar vein of each captured individual for sex typing.

At least two persons spent 7 nights per month in our study site censusing owls and searching for tree cavities. The crowns of the canopy trees in our study site are umbrella shaped with leaves