**Research Article for Biology Letters**

# Experimental vacancies do not induce settlement despite habitat saturation in a cooperative breeder

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**Running head:** vacancies do not induce settlement

**Key-words:** ecological constraints, ecological trap, perceptual trap, Malurus

## Abstract

The paradox of cooperative breeding whereby individuals assist others instead of reproducing independently is generally explained through ecological constraints, but experimental evidence is scant. Here we performed the crucial test of the role of habitat saturation through experimental creation of vacancies and find that despite abundant presence of potential mates, subordinates are reluctant to disperse into suitable vacant habitat where conspecifics are absent. We argue that sudden disappearance of multiple group members might indicate a heightened risk of predation. Thereby the results of this study are consistent with the 'perceptual trap' hypothesis: the avoidance of habitats because cues do not accurately reflect their quality. Interestingly, this hypothesis can also explain previous findings, which were widely interpreted as evidence for ecological constraints as a driver of cooperative breeding. Our results can have considerable implications for conservation as it means that opportunities for colonization might go unexploited.

## Introduction

In cooperatively breeding species individuals assist others with raising offspring rather than breeding on their own [1,2]. In most cooperatively breeding species delayed dispersal underpins helping behaviour. Extrinsic factors limiting dispersal or independent breeding have now widely been accepted as an explanation for the evolution of delayed dispersal. Such ecological constraints can consist of limited availability of suitable habitat [e.g. 3], low probability of finding a mate [e.g. 4,5], high risk of mortality associated with dispersal and independent breeding [e.g. 6,7], and a low chance of successful independent breeding [e.g. 8,9]. A rigorous test of the role of limited availability of habitat and mates was provided by the creation of breeding vacancies through removal of group members in the cooperatively breeding superb fairy-wren (*Malurus cyaneus*). In this species, all male offspring delay dispersal for at least one year to assist the dominant pair, whereas female offspring show obligate dispersal after reaching independence at 1 year of age [10]. Thus high risk of mortality associated with dispersal cannot explain cooperative breeding in this species. Neither can low chance of successful independent breeding, since fairy-wrens are facultative cooperative breeders The experiment showed that no dispersal occurred in the 2-to-3 days following creation of a breeding vacancy by removal of an unassisted pair, but when the breeding female was released, a neighbouring male subordinate immediately dispersed to pair with her. This has been interpreted as showing that under conditions of habitat saturation both a shortage of mates and limited habitat promote delayed dispersal, whereas when there were territorial vacancies the shortage of mates itself was sufficient to promote delayed dispersal [11]. Although this study has become a textbook example [12–16] of the role of ecological constraints in cooperative breeding, a crucial test involving a species where mate limitation can be excluded as a factor has thus far been lacking. Here we performed such an experiment in a sister species to the model system of the original experiment, the red-winged fairy-wren (*M. elegans*). This species shares most aspects of social organisation and mating system with *M. cyaneus*, but has one remarkable difference, which is that both sexes delay dispersal and help. Thus, there never is a shortage of adults to fill breeding positions, so such a shortage cannot explain delayed dispersal [17].

## Results & Discussion

We experimentally created vacancies using permanent translocations (>10km away) with two different treatments. First, to test whether the limited availability of suitable habitat itself can promote delayed dispersal, seven pair vacancies were created by removing all group members from their territory before the onset of the breeding season. Similar to the previous experiment on *M. cyaneus*, where the lack of dispersal was explained by the limited availability of mates, we found that despite the presence of subordinates of both sexes nearly all vacancies remained unclaimed. Of the seven created vacancies, only one was filled by a neighbouring subordinate male and a female from unknown origin, which dispersed three days after creation of the vacancy. Of the remaining six vacancies, five largely remained vacant for the rest of the breeding season, though parts of the vacated space were sometimes eventually usurped by neighbours. One vacancy was eventually filled by a neighbouring dominant female who divorced her mate and paired up with a subordinate from another neighbouring territory, 24 days after relocation. At first sight, these results suggest that the availability of suitable habitat itself is not the main driver for delayed dispersal in this species.

In our second treatment, single sex vacancies (N=4 male, N=3 female vacancies) were created by relocating either males or females from a territory, to confirm that dispersal can be experimentally initiated. Each of the seven vacancies was filled up on average within 1.6 ± 0.7 S.E. days (range 8hrs- 4.9 days) after relocation, and this was significantly more often than the pair vacancies (Figure 1, Fisher's exact test $P<0.001$). For four dispersers their location of origin was known and these were all immediate neighbours, the remaining three were unringed and thus their location of origin could not be determined, although two of these were not an immediate neighbour.

Unexpectedly, our results perfectly match the earlier relocation experiment in the closely related *M. cyaneus*, where it was argued that a lack of mates could drive delayed dispersal, even when suitable habitat was available. We now show that even in the absence of mate limitation, birds might be reluctant to disperse to vacant suitable habitat. We suggest five ideas that could explain these results.

First, the subordinates surrounding the vacancies might have been reluctant to pair up, because they were closely related or genetically incompatible [18]. However, our long-term data shows that such an explanation is rather unlikely, because many social pairs are in fact closely related and avoid inbreeding through extra-group paternity [19]. Furthermore, in three instances a subordinate male and female that were repeatedly observed in the vacancies, but did not claim these, eventually paired up with each other respectively one month, two years and three years later. The subordinates (from different groups) that paired up a month later did so by occupying parts of existing territories and established their new territory on one side bordering the vacancy. Finally, in two of the experimental removals the individual claiming the vacancy was not an immediate neighbour, and natural data shows that although most individuals move to a neighbouring vacancy, dispersal can occur over several territories (mean ± S.D territory widths: females: 3.6 ± 3.0, N=116; males: 1.4 ± 0.7, N=91), suggesting that the pool of potential dispersers is not confined to immediate neighbours only.

Second, lack of awareness of the existence of the pair vacancies might have prevented dispersal. This is also an unlikely explanation as birds were observed to make forays into the vacant areas, as soon as 5.5 hours after creating the vacancy. Within the first 5 days after relocation 59 forays of at least 33 different individuals were observed in the vacancies. Thirty individuals could be identified, with the majority (60%, 18/30) being observed in the same vacancy at different occasions (up to three times). Most of the identified individuals on forays were male (N=10) and female (N=7) subordinates from the immediate vicinity (from neighbouring groups or two territories away), although interestingly male (N=8) and female (N=5) dominants from the immediate vicinity were also observed in the vacancies. In two cases where males were removed, a male was observed in the vacancy in close proximity to the unpaired female, but did not stay there. One of these males was displaying to the unpaired female and identified as a dominant from a neighbouring territory. Individuals on forays typically moved quietly through the area, and thus our observations are likely an underestimation of the forays that actually took place.

Third, a vacancy without an experienced breeder might not be attractive enough to trigger dispersal as both individuals would be inexperienced and unfamiliar with the territory.

Yet, our natural long-term data shows that new territories are formed by subordinates, although it is quite rare (on average 1.1 territory per year). Furthermore, this does not necessarily include parts of the (familiar) natal territory, but usually happens through usurping parts of existing territories. Unfortunately, we do not have a good idea how such new territories are formed, i.e. whether pairs form before occupying a territory or the other way around. This is likely largely due to the rapidity of the events. In one case a subordinate was observed in its natal territory 3hrs before being observed defending a newly established territory with a female subordinate, respectively two and three territories away from their natal territory. Recent work also suggests that subordinates should disperse, because the annual fitness (measured as reproductive value) of dominants is 30-40% higher compared to those of subordinates [20]. At the same time, by leaving the group, the reproductive values of the remaining group members will generally increase due to reduced competition [20]. Together, these fitness benefits are much larger than the marginal indirect benefits of staying (i.e. the combined change in reproductive values of group members from one group size to the next, diluted by the relatedness to the subordinate [20]). Since red-winged fairy-wrens are long lived, these annual fitness payoffs will accumulate over time, while it also means that the availability of vacancies is rare. Altogether, these arguments suggest that subordinates should disperse while they can.

Fourth, a single subordinate might simply not be capable of holding a territory alone while trying to attract a mate. Again, the rapidity of events with which single sex vacancies are filled and new territories are established means single subordinates holding a territory have not been observed under natural conditions. At the same time, this short time window over which vacancies are filled and forays by subordinates in the vacancies were observed suggests this explanation is rather unlikely and any costs associated with defending a territory alone are expected to be extremely short term. However, more complicated experiments are necessary to be definitive.

Fifth, the available vacancies might have been deemed unsuitable by prospective dispersers. Since single vacancies are filled up so quickly, abrupt loss of all the residents on a territory are likely to be rare under natural conditions. Although our long-term data shows that both individuals of a pair have been replaced between breeding seasons, the exact timing of such events is unknown. The rapidity with which single sex vacancies are filled up suggest that a vacant territory can only arise in the unlikely event that both pair members die on the exact same day. The experimental creation of pair vacancies, which resulted from the ‘sudden disappearance’ of a breeding pair, could thus be perceived to be an indication of a heightened risk of predation. Despite their high survival [20], predation risk is an important factor contributing to extrinsic mortality for adult fairy-wrens [21] and these species have a suite of typical alarm and mobbing vocalizations that they give in response to aerial and terrestrial predators [21,22]. Thus, the absence of conspecifics might be used as a source of public information and deter individuals from dispersing to vacant habitat.

The use of public information has frequently been shown to be used for settlement decisions [23] including in fairy-wrens [10]. However, this usually works in opposite direction with individuals being attracted to conspecifics [24,25] or habitat patches with high reproductive success or parental feeding activity [26–29]. The observation that individuals avoid habitat that would have generated fitness benefits has recently been described as undervalued resource’[30] or a ‘perceptual trap’ [31]. However, experimental evidence for this phenomenon has been scarce, as the main difficulty is to test that fitness would have been higher if the avoided habitat would have been chosen. In lesser prairie chickens (*Tympanuchus pallidicinctus*) it was shown that habitat treated with herbicides which resulted in defoliage of shrubs was avoided, though such habitat did not have reduced nesting success [31]. However, potential reduced adult survival could not be excluded as an explanation of avoidance of these areas [31]. Our results that subordinates forgo the opportunity to breed independently in suitable habitat now provides experimental evidence for the perceptual trap hypothesis. Such effects can have considerable implications for conservation as it means that opportunities for colonization go unexploited. To conclude, our study shows that results from a previous experiment what seemed to be clear evidence for habitat saturation and mate limitation may have an alternative or additional explanation. More complicated experiments will be necessary to tease these alternatives apart.

## Methods

The relocation experiment was conducted as part of an ongoing study on red-winged fairy-wrens (*Malurus elegans*) in Smithbrook Nature Reserve and surrounding state forest in Western Australia (34°20′S, 116°10′E) in 2014 and 2015 [20]. The main study area comprises ~65 red-winged fairy-wren territories of which >99% of the adult birds are individually colour-banded with permission from the Australian Bird and Bat Banding Scheme. In addition, in another ~30 territories surrounding the main area 80% of the birds are individually colour-banded (for more details see: [32]). Dispersal has been observed to occur both during and outside of the breeding season (L. Brouwer, unpublished data). Before the onset of the breeding season all territories were checked for the status and presence of birds. Social status of group members was determined from behavioural observations, variation in plumage and age [17,33], with each group comprising a 'dominant' pair-bonded male and female and up to six subordinate male and/or female helpers. Relocation territories were selected as those inhabiting pairs or a pair with a single subordinate, surrounded by territories with subordinates (potential dispersers). In the mornings of 9-14 October 2014 pair vacancies were created by removing all group members from their territories (N=5 pairs, N=2 pairs with a single subordinate). In the mornings of 9-15 October 2015 single sex vacancies were created either through removing a single bird from a territory (N=3 males, N=3 females from six pairs) or through removal of both the dominant and subordinate male (N=1 group). Since for both treatments similar types of territories were selected, territory quality cannot explain the difference in dispersal rates between the treatments. Furthermore, there was no difference in the overall presence of subordinates (i.e. potential dispersers) in the population between the pair (mean ± S.D. males: 0.89 ± 0.98, females: 0.46 ± 0.70) or single sex vacancies (mean ± S.D. males: 0.69 ± 0.86, females: 0.41 ± 0.69). Data are deposited at the Dryad Digital Repository [34].

Birds were caught using mist nets, but without the use of a playback to avoid attraction of potential dispersers. Territories were randomly selected with respect to sex of the removed bird, and in case both individuals were caught we immediately released the partner of the focal bird back into its territory. The removed birds were released in pairs/groups in suitable habitat >10km away. None of the relocated birds returned to the study area. All procedures were approved by the Australian National University Ethics committee and the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA). After relocation experimental territories were checked at least twice a day until the vacancy was filled (birds vocalizing and defending the territory and showing pair-interactions like allopreening) or in the case of unclaimed vacancies twice a day for the first week, daily in the second week and bi-weekly thereafter.

## Acknowledgements

The Western Australian Department of Biodiversity, Conservation and Attractions (DBCA) and the ANU Animal Experimentation Committee gave permission for fieldwork and sampling. The Australian Bird and Bat Banding Scheme gave permission for colour-banding. We thank Adrian & Julia Wayne and other staff of the DBCA Science division in Manjimup, John Angus and Karen & Michael Keely for logistical support and hospitality. We are grateful to Marina Louter, Julia Gulka, Edward Jenkins, Nadia Hijner, Bas Kok, Kirsty MacLeod, Javier Cotin and Sarah Dobney for assistance in the field.

## Funding

The work was supported by fellowships and grants from the Australian Research Council awarded to LB (DE130100174) and AC (DP0451018, DP1092565).

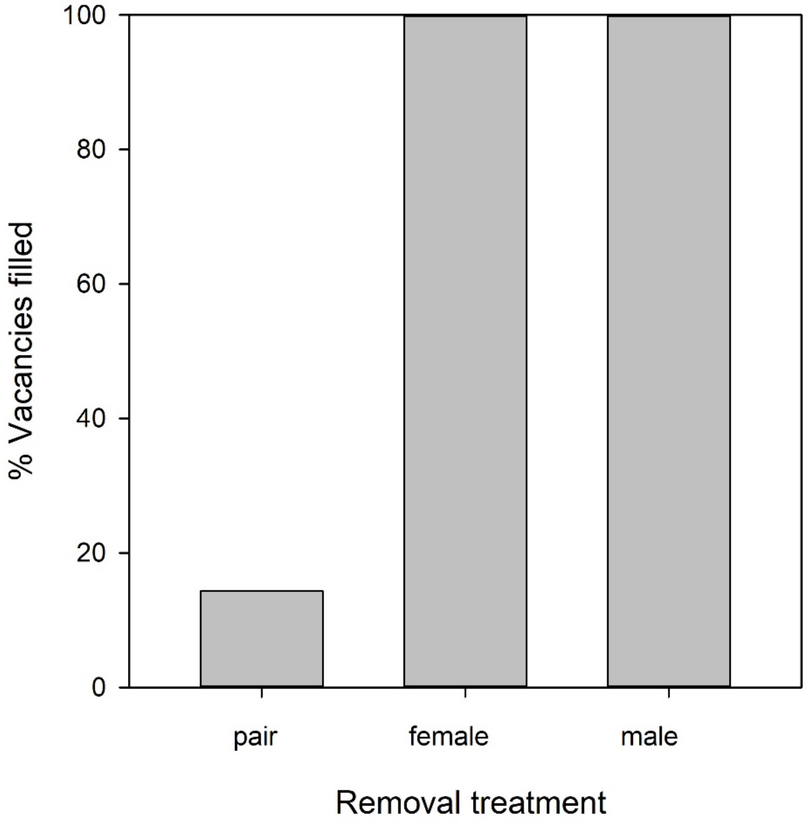

**Figure 1.** The percentage of vacancies filled after experimental removal of pairs, females and males in red-winged fairy-wrens (*Malurus elegans*).

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