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Empirical evidence for ecological traps: a two-step model focusing on individual decisions

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Abstract Ecological traps are poor quality habitats that are preferred by individuals and that cause standard indicators of habitat quality (e.g., density, age structure, order of settlement) to be misleading. A maladaptive choice of habitats may have detrimental effects on individual fitness and long-term population persistence. For conservation purposes, it is therefore critical to identify ecological traps. We discuss a recent review on the relationships between density, reproductive success and productivity at the patch level. We also discuss the concept of ecological traps and definitions of habitat quality and habitat preference. Based on recent literature on ecological traps, we argue that no study shows evidence of an ecological trap in its strict sense, i.e., a preference for sink and an avoidance of source habitat. This lack of evidence is partly due to poor measures of preference and individual fitness, and to an absence of studies at the individual level. We suggest a two-step protocol at the level of individuals to investigate ecological traps by linking: (1) habitat characteristics, i.e., potential cues used by individuals, to fitness, and (2) preference for specific habitat characteristics. This protocol is illustrated by a long-term study on breeding territory selection in Northern Wheatears (*Oenanthe oenanthe*) in Sweden. Using our protocol, we could determine at least in part why Wheatears show a mismatch between habitat preference and fitness. We conclude that there is an urgent need for more studies on individual habitat-selection decisions before we can find less labour-intensive ways to identify potential trap situations.

Introduction

The knowledge of habitat quality is at the core of avian ecology and conservation. Local density (or relative abundance) is the most commonly used indicator of habitat quality in conservation biology studies, probably because it is a time-efficient parameter to quantify in a variety of situations. However, the use of density as an indicator of habitat quality has been strongly criticized since the seminal paper of Van Horne (1983). For example, density may fail to predict breeding habitat quality when population sizes are determined in other habitats (e.g., in winter habitats) and when dominant individuals settle in prime habitats by displacing subordinates, leading to aggregations in poor habitats (for more examples, see Garshelis 2000). Furthermore, human activities causing rapid conversion of pristine landscapes, the introduction of exotic species, or the supply of novel resources in food webs, have created new habitat types that may be preferred but actually are poor habitats in terms of reproduction and survival (i.e., ecological traps). Thus, counting birds to estimate habitat quality may be misleading.

Here, we briefly review what is known about the relationship between density and reproduction and then focus on the concept of ecological traps and non-ideal habitat selection in general, and how to identify them. We suggest

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a two-step protocol to identify non-ideal habitat selection and its causes, focusing on individual selection decisions and habitat-specific demography. We illustrate this protocol with data from a long-term population study on breeding habitat selection and habitat-specific demography in a population of Northern Wheatears (*Oenanthe oenanthe*) in Sweden.

Density as an indicator of habitat quality

Although, in theory, density may be a poor indicator of habitat quality, empirical data may suggest otherwise. To test whether density may be used as a surrogate for habitat quality, Bock and Jones (2004) reviewed 109 studies of 67 bird species breeding in a natural setting (i.e., omitting nest box studies) with data on local densities, per capita reproduction and productivity (i.e., density × per capita reproduction). Productivity was used because habitats with equal per capita reproduction but higher density are more productive, and therefore could be argued to be more valuable in terms of conservation (see also Van Horne 1983). In general, the results suggest a broad positive association between local density and individual reproductive success, as 72% of the studies showed higher individual reproductive success in the high- compared to low-density habitats. Accordingly, this relationship was stronger for estimates of productivity: 85% of the studies showed high-density habitats to also have higher productivity. So is it time to relax the critique against using density as an indicator of habitat quality?

No, several facts suggest that we still need to be cautious about using density to evaluate habitat quality. As recognised by Bock and Jones (2004), these results have to be considered with caution because they are based on vote counting (i.e., counting the number of positive and negative relationships without taking into account effect size or *P*-values) and many associations considered in these calculations were non-significant. Furthermore, the analysis did not take into account the repeated structure of observations (several species occurred more than once), temporal trends in publication biases, and phylogenetic relationships among species (Arnqvist and Wooster 1995). Although comparisons of density–reproduction relationships based on a single year do not separate the effects of ordinary density-dependence in reproduction from ecological traps, about 28% of the studies suggested negative relationships between density and reproductive success. Most importantly, there were some indications that these studies were located in highly disturbed landscapes (Bock and Jones 2004). Because many threatened and red-listed species inhabit disturbed landscapes, and because ecological traps are especially likely to occur in such environments, it is

still relevant to question whether density alone should be used to identify "high quality" sites for conservation purposes. It is worth mentioning that productivity is not necessarily a better indicator of habitat quality than density, because productivity estimates may actually hide ecological traps (i.e., an attraction to "poor quality" habitats resulting in higher densities compensates for lower per capita reproduction).

The ecological trap concept and its definitions

There has been an increased theoretical and empirical interest in ecological traps: no fewer than four reviews have addressed this topic since 2002 (Schlaepfer et al. 2002; Battin 2004; Robertson and Hutto 2006; Gilroy and Sutherland 2007). Although there are slight differences in the definitions of ecological traps presented in these papers (cf. Robertson and Hutto 2006 vs Battin 2004), it is generally agreed that ecological traps occur when individuals assess habitat quality using cues that are no longer linked to the true quality of the habitat, such that "poor quality habitats" are preferred over "high quality" ones. Thus, the observed preferences deviate so strongly from an ideal habitat selection expectation that the relationship between habitat preference and habitat quality becomes negative (Fig. 1). This implies that an ecological trap is an extreme situation at one end of a continuum ranging to ideal habitat selection (i.e., a perfect match between habitat quality and preference) at the other end (Kristan 2003; see Fig. 1). Hereafter, we will refer to intermediate levels of deviation from ideal selection as non-ideal habitat selection (cf. "equal preference" traps in Robertson and Hutto 2006; Fig. 1).

Even though various authors agree on a general definition of the ecological trap concept, there are still some ambiguities concerning its details and its testing, including the definition of habitat quality and the measurement of habitat preferences. Habitat quality should be measured in terms of its direct effects on individual fitness (Morrison et al. 1992). The use of "suitability" (Schlaepfer et al.
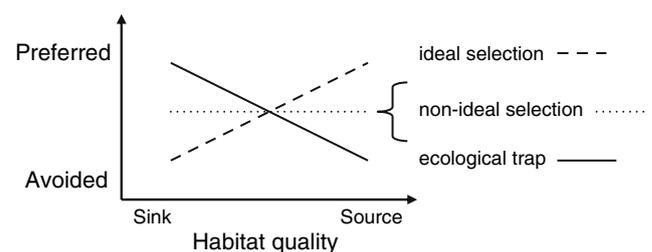

Fig. 1 Schematic figure on the relationships between preference and habitat quality (sources and sinks). Each *line* reflects a potential type of habitat selection (i.e., ideal, non-ideal, and ecological trap)

2002) or "relative habitat quality" (Robertson and Hutto 2006) as a surrogate for breeding habitat quality either include density-dependent effects on fitness (see Fretwell and Lucas 1970) or do not take into account the fact that habitats may produce a surplus (source) or a deficit (sink) of individuals. Consequently, such definitions of habitat quality may fail to identify what we suggest are true ecological traps (i.e., a preference for sink habitats; see also Gilroy and Sutherland 2007). For example, it is questionable whether we would consider a preference for the poorer of two source habitats as an ecological trap when both habitats produce a surplus of individuals. Such minor deviations from ideal habitat selection are probably frequent in nature owing to common habitat selection constraints concerning spatial selective range, ability to discriminate small differences in quality, and search costs (Lima and Zollner 1996). Similarly, a preference for habitat patches that have a negative population growth due to density-dependence (i.e., a pseudo-sink; Watkinson and Sutherland 1995) should not be viewed as an ecological trap if densities in all habitats are high. Therefore, we support the definition used by Battin (2004) whereby habitat quality should be viewed in terms of local population growth (lambda), where some habitats are sources ($\lambda > 1$) and others are sinks ($\lambda < 1$) also at low population densities. Kristan (2003) extended this view to single territories in mosaic landscapes where some territories produce an excess and others a deficit of individuals. This individual based source–sink definition is simple, distinct and it gives clear predictions of its consequences for population growth and long term persistence (see Kristan 2003). Other definitions and other extensions (e.g., "severe" traps, "equal preference" traps or density traps; Robertson and Hutto 2006) are too vague or may only cause confusion, because they may either refer to cases of less extreme, non-ideal habitat selection or to pseudo-sinks with ideal habitat selection (Kristan 2003).

If habitat quality is difficult to estimate in nature, it may be even harder to estimate habitat preference. Ideally, habitat preferences should be investigated by choice experiments but this proves to be very labour-intensive or even unrealistic. Robertson and Hutto (2006) therefore listed all previously used measures of habitat preference: proportion of dominant individuals, temporal variation in population size (populations in preferred habitats vary less in size), order of establishment, site fidelity patterns and density. Although all measures have their drawbacks (see Robertson and Hutto 2006), the closest alternative to experiments would be to use realised preferences such as order of choice (mainly species reoccupying sites annually) or patterns of site fidelity/infidelity.

Of 45 studies reviewed in Robertson and Hutto (2006), only 7 used either an experimental protocol (insect studies) or settling dates (birds) to estimate preference. Almost all studies used habitat patch averages to estimate habitat preference or fitness relations. According to the source–sink definition of ecological traps, no study on birds has unequivocally identified an ecological trap. Furthermore, the use of incomplete data to assess individual fitness (e.g., only reproduction) opens the possibility of fitness compensation (Battin 2004) in many studies.

Hence, a strong conclusion from the review by Robertson and Hutto (2006) is that it is not easy to investigate ecological traps. Another conclusion is that very few studies have attempted to investigate ecological traps in terms of individual habitat selection decisions. Instead, most studies have compared habitat patch estimates of preference (e.g., average breeding time or age of breeders) and demography (see Robertson and Hutto 2006). Because such comparisons only give averages across habitats and, thus, do not capture individual variation in habitat selection decisions, we suggest an alternative protocol for testing ecological traps and other habitat selection scenarios that has the potential to elucidate the causes of an observed mismatch between preference and habitat quality.

Non-ideal breeding habitat selection in Wheatears

Since 1993, we (T.P. and D.A.) have studied breeding habitat selection in a population of Northern Wheatears (*Oenanthe oenanthe*) in an agricultural landscape (59°50′N, 17°50′E) of south-central Sweden. The landscape consisted of a mosaic of grazed and ungrazed grasslands (11%), crop fields (68%), and woodlands and forest (21%). Territory sites, i.e., sites previously occupied by Wheatears, were spatially scattered and located in grasslands (58%), crop fields (28%) and on farmyards (13%), either solitary (on average 30%; mainly in fields and on farms) or in small clusters of 2–5 sites (70%; mainly in grazed grasslands).

Wheatears are small, long-distance tropical migrants. They are insectivorous ground-foraging birds with a main distribution in habitats consisting of short field layers (i.e., vegetation layer consisting of grasses and herbs; Cramp 1988). Previous studies show that Wheatears have a higher breeding success in habitat patches with short than tall field layers, probably as a result of higher prey availability and lower risk of nest predation in short field layers (Tye 1992; Pärt 2001a, b). In our study area, territories with short and tall field layers were spatially mixed in a mosaic (for more details, see Pärt 2001a, b; Arlt and Pärt 2007).

In order to test whether habitat selection by individual Wheatears deviated from an ideal habitat selection, we used a two-step protocol at the individual level (Fig. 2). First, we tested which habitat characteristics were linked to

components of individual fitness (i.e., subsequent survival and production of local recruits). As the effect of habitat on individual fitness is mainly determined at the territory scale in this species, we examined the relationships between territory characteristics and these two fitness components. Second, we tested the links between territory characteristics and male territory preference. To estimate territory preference, we used the order of territory establishment in spring. We only investigated preferences of individuals choosing new breeding sites, i.e., those displaying site fidelity between years were omitted. By using this protocol, we could identify an ecological trap or non-ideal habitat selection when territory characteristics linked to individual fitness were negatively related or uncoupled to male preference, respectively (see Fig. 2). For example, if field layer height is a good predictor of individual fitness and the difference in field layer height between territories causes some territories to act as demographic sinks whereas others

Fig. 2 The two-step individual model of habitat selection by Northern Wheatears (*Oenanthe oenanthe*) (**a**), and two of its potential outcomes (**b**). **a** Step 1: testing whether habitat characteristics (potential cues used by individuals) are linked to individual fitness (or population growth). Step 2: testing whether the same habitat characteristics are linked to individual preference (e.g., order of establishment). **b** Relating habitat characteristics to preference will determine whether habitat selection is ideal (shown), non-ideal (not shown) or an ecological trap (shown). Note that a preferred habitat characteristic that is unrelated to individual fitness suggests a case of non-ideal selection

act as sources (i.e., a strong link in step 1 covering the variation from a sink to a source; Fig. 2), a preference for the sink type of habitat (i.e., step 2; Fig. 2) would strongly suggest a true ecological trap (see Fig. 2b). On the other hand, equal demographic rates with respect to field layer height in territories (i.e., no link in step 1), but strong preference for short field layers (i.e., a significant link in step 2), would suggest a case of non-ideal selection (this type of non-ideal selection is not shown in Fig. 2). By linking many different territory characteristics to data on individual demographic rates and territory preferences, we also could potentially identify which cues individuals may use when assessing and selecting territories and habitat characteristics. Here, we report results based on two territory habitat characteristics, namely field layer height (short vs tall) and the number of neighboring territory sites (i.e., sharing borders with the focal territory site; for a more exhaustive testing of territory characteristics, see Arlt and Pärt 2007).

The only significant predictor of individual fitness was territory field layer height; birds breeding in territories with permanently short field layers produced significantly more recruits than those breeding at sites with field layers that grew tall (e.g., ungrazed pastures or crop fields). Adult survival rate (as estimated by high quality data on return rates; see Arlt 2007) did not differ between these two habitat categories (Fig. 3). Furthermore, a matrix population model suggested that territories with short field layers acted as sources whereas those with tall field layers acted as demographic sinks (Arlt 2007). The difference in habitat-specific lambda between these two habitat types was dramatic, about 0.25 (Arlt 2007). Thus, by using field layer heights as an indicator of habitat quality, we had a perfect set-up to investigate habitat selection scenarios ranging from ideal to non-ideal selection and true ecological trap. However, male preference of territory sites, as estimated by order of establishment, was unrelated to territory field layer height. Instead, the Wheatears preferred territories located in clusters (Arlt and Pärt 2007), a characteristic that was unrelated to demographic rates. Clearly, there was a mismatch between observed preference and quality in terms of expected individual fitness, and this mismatch could not be explained by fitness compensation. This mismatch did not, however, result in a negative relationship between preference and quality (i.e., ecological trap). Thus our data show a case of non-ideal habitat selection where (1) territory characteristics linked to fitness were uncoupled from preference, and (2) territory characteristics linked to preference were uncoupled from fitness.

The Northern Wheatear has an evolutionary history of inhabiting open habitats characterized by bare ground or short field layers (Cramp 1988). One may therefore ask why Wheatears do not prefer permanently short field layer
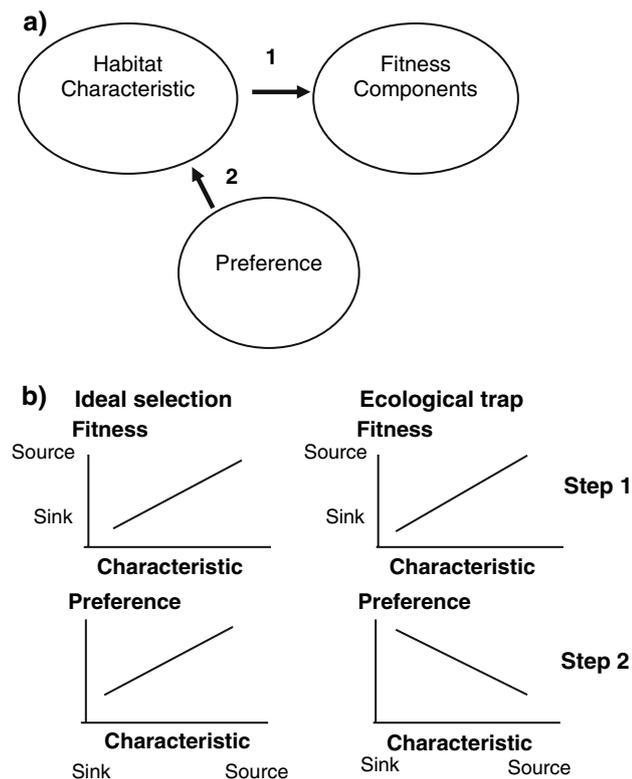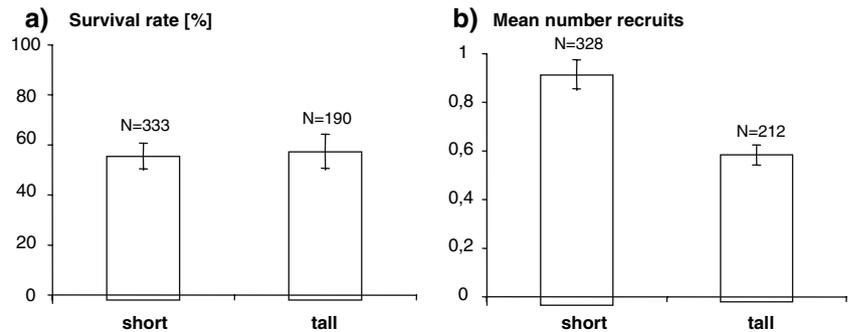
Fig. 3 Male survival probability (±95% confidence intervals) (**a**), and mean number of recruits (±SE) produced in relation to territory field layer height class (**b**) for breeding Northern Wheatears (from Arlt and Pärt 2007)

habitats in the farmland. One possibility is that individuals are unable to identify these habitats at the time of territory establishment in spring. In fact, at the time of arrival to the breeding grounds, almost all individuals choose to settle at sites with either bare ground (i.e., crop fields, farm yards) or short field layers (cut grasslands and grasslands grazed in the previous summer/autumn). However, at 50% of the sites with bare ground or short field layers in early spring, field layers grew tall and dense at the time young were fed, i.e., when the effect of field layer height is most marked (Pärt 2001b). Thus, our data suggest that one cause for the observed uncoupling between territory preference and territory quality was a temporal mismatch of the cue used to assess habitat quality. The observed preference for territory aggregations, however, remains enigmatic (for a discussion, see Arlt and Pärt 2007).

Conclusion

Because they are caused by maladaptive habitat selection behaviors of individuals, ecological traps should be empirically tested using individual decisions. Our two-step protocol linking realized territory preferences, territory characteristics and fitness components has several advantages compared to previous methods of testing habitat selection scenarios. Most importantly, it pinpoints potential cues involved in the selection of breeding territories and tests whether these cues also are good predictors of territory quality. Furthermore, the protocol may help determine the reasons behind mismatches or negative relationships between habitat preference and individual fitness. For example, by investigating field layer structures at the time of establishment and during the nestling phase, we were able to understand why this potential cue used by individuals was not predicting habitat quality later on in the breeding season and why individuals therefore did not prefer permanently short field layers. The identification of habitat selection cues involved in ecological traps and knowledge of underlying mechanisms for the observed mismatch between preference and fitness are crucial when

designing conservation strategies to avoid a deterministic extinction (see also Gilroy and Sutherland 2007). For example, making nesting sites (i.e., stone piles) in crop fields inaccessible and letting ungrazed grasslands reach high field layers in early spring (i.e., by preventing grazing after cutting) would result in a good match between preference and fitness in Wheatears.

Detailed demographic data, as described here, are admittedly extremely difficult to obtain from wild populations in most taxa, except possibly for birds. Therefore, the main challenge for the future is to find approaches that are more time-efficient than detailed population studies of individuals to identify ecological traps. For example, a negative relationship between the proportion of dominant individuals (e.g., old birds with adult plumage in species with delayed plumage maturation) and productivity at the patch level could serve as one indicator of an ecological trap (Weldon and Haddad 2005). However, before such ecological trap indicators can be used, we need more detailed studies of habitat selection at the level of individuals and habitat patches to validate their predictive power.

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