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Pair formation among experimentally introduced mallards *Anas platyrhynchos* reflects habitat quality

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Using data from two independent field experiments, we address whether pair formation in introduced mallards *Anas platyrhynchos* is associated with habitat quality, specifically food limitation at the brood stage. Based on the concentration of total phosphorous in the water, the study lakes were divided into two groups, 'poor' and 'rich'. In one of the experiments we used mallard ducklings imprinted on humans to study mass change of ducklings in poor and rich lakes, respectively. It turned out that ducklings foraging on poor lakes gained less mass than ducklings foraging on rich lakes, the division of lakes thus reflecting habitat quality at the brood stage. Introduced mallards formed heterosexual pairs on lakes that were, in a relative sense, high-quality brood habitats, whereas they did not on lakes of low-quality brood habitat. Pair formation thus seemed to reflect the suitability of habitat for breeding.

Introduction

Food shortage is an important aspect of habitat quality influencing life history traits (Martin 1987) and several population and community level processes (Wiens 1989, Boutin 1990, Newton 1998). In a series of experimental studies, we addressed the role of food in habitat selection and distribution of breeding mallards *Anas platyrhynchos* (Pöysä *et al*. 1998, 2000, Sjöberg *et al*. 2000). In an introduction experiment, we tested the hypotheses of conspecific attraction (Stamps 1988) and ideal preemption (Pulliam & Danielson 1991) in habitat selection of nesting mallards (Pöysä *et al*. 1998; *see also* Elmberg *et al*. 1997). We found that in some lakes introduced birds attracted wild conspecifics arriving from spring migration, whereas in other lakes they did not.

In another field experiment focusing on habitat quality, specifically food limitation at the brood stage, we found that some lakes were inferior brood habitats and that habitat quality at the brood stage may affect the distribution of nesting pairs (Sjöberg *et al*. 2000). We also found that, independent of treatment, the outcome of the introduction experiment was at least partially dependent on the quality of the lakes as brood-rearing habitats (Pöysä *et al*. 2000).

Hence, habitat quality seems important to processes at individual as well as at population level in breeding mallards. In the introduction experiment, we observed variation in pair formation among introduced mallards. On some lakes, they split up into pairs, whereas on other lakes they did not. In this paper, we focus on this variation. By using data from two independent field experiments, we ask whether pair formation among introduced birds is associated with habitat quality, specifically food limitation at the brood stage.

Material and methods

This analysis is based on data gathered in two independent field experiments that have been reported in full elsewhere (Pöysä *et al*. 1998, Sjöberg *et al*. 2000). Both were done in the Umeå area, central Sweden (about 63°30´N, 20°E; map given in Elmberg *et al*. 1993: fig. 1), an area situated in the mid-boreal zone, and being rich in lakes and wetlands. Lakes are ice-covered in winter and the selection of nesting lakes is repeated each spring by migratory mallards. As details of the experimental procedures can be found in the original articles we here report on the most pertinent parts only.

In a two-year introduction experiment (Elmberg *et al*. 1997, Pöysä *et al*. 1998), we used captive-bred, pen-raised and wing-clipped mallards obtained from the Swedish Sportsmen's Association from two breeders in Södermanland, south-central Sweden. The ducks arrived at Umeå in March, 6–8 weeks prior to release so that they were able to adjust to the local light regime. All birds were treated identically, and they were kept in one big group in an unheated indoor pen and fed a combination of poultry pellets, whole barley and vitamins *ad libitum*. Using a cross-over design, we introduced six individuals (3 males and 3 females) randomly selected from the big group to each lake in spring just before the arrival of migrating wild mallards, i.e. between 2 and 6 May 1993 (16 lakes) and 1 and 4 May 1994 (16 other lakes) (Elmberg *et al*. 1997, Pöysä *et al*. 1998). Each lake received introduced mallards in one year only, the other year serving as a control in the introduction experiment (Pöysä *et al*. 1998; *see* also Elmberg *et al*. 1997). In both years, we censused introduced as well as wild mallards on the lakes. Two censuses were done in both years in the early part of the breeding season (8–21 May). Pair formation among the introduced birds was monitored and the number of separate pairs was recorded in each census. Observers were not aware of the lake classification (*see* next paragraph) at the time of censuses. Heterosexually paired birds close together, keeping a distance to other mallards, introduced or wild, were used as a qualitative definition of a pair; in practice, pair formation was obvious in the field. Sustained proximity to a member of the opposite sex has been used as a criterion to determine pair status also in other studies (e.g. Wishart 1983, Hepp & Hair 1984, Johnson & Rohwer 1998). We used the mean of the two censuses for the total number of introduced birds, the number of separate pairs, and the proportion of birds in pairs as dependent variables.

In the other experiment conducted in June 1996, we used mallard ducklings imprinted on humans to address brood-stage food limitation by studying mass change of ducklings (Sjöberg *et al.* 2000). Based on the concentration of total phosphorous in the water, the study lakes were divided into two groups; 'poor' and 'rich'. Total phosphorous is a reasonably good indicator of the trophic status of lakes (Kerekes *et al.* 1990, Staicer *et al.* 1994, Jeppesen *et al.* 2000). From a group of 31 four-day-old mallard ducklings we randomly selected 12 to always be used in poor-lake foraging trials and another 12 to always be used in rich-lake foraging trials, the seven remaining ducklings being used as controls. All 31 ducklings were kept in a pen with free access to food when not in experimental trials. On each experiment day the food was taken away at 8 a.m. and the 12 ducklings of both experiment groups were collected for daytime foraging trials, the 7 control ducklings remaining in the pen with access to food. One trial was run per lake and parallel trials were run on the same days on a poor lake (n = 11) and a rich lake (n = 11). Each trial lasted 6 hours, usually starting at 10 a.m., and each duckling, including the controls, was weighed before and after the trial. After trials the ducklings which had been foraging on lakes were brought back to the pen, and all 31 ducklings were kept together there with free access to food until the beginning of the next day's trial. It turned out that ducklings foraging on poor lakes gained significantly less mass than ducklings foraging on rich lakes (Sjöberg *et al.* 2000). Poor lakes were thus clearly inferior to rich lakes as brood habitat.

For the present analysis we used data from lakes used in both of the aforementioned experiments. In all, we had 14 such lakes, seven of them being poor lakes and the other seven rich lakes according to Sjöberg *et al.* (2000). Because introduced birds disappeared from one poor lake and from one rich lake (*see also* Elmberg *et al.* 1997, Pöysä *et al.* 1998), the final sample size was six for both lake types. We used the Mann-Whitney U-test in comparisons between poor and rich lakes. Analyses were run with SYSTAT procedures (Wilkinson 1992). Probability values are two-tailed.

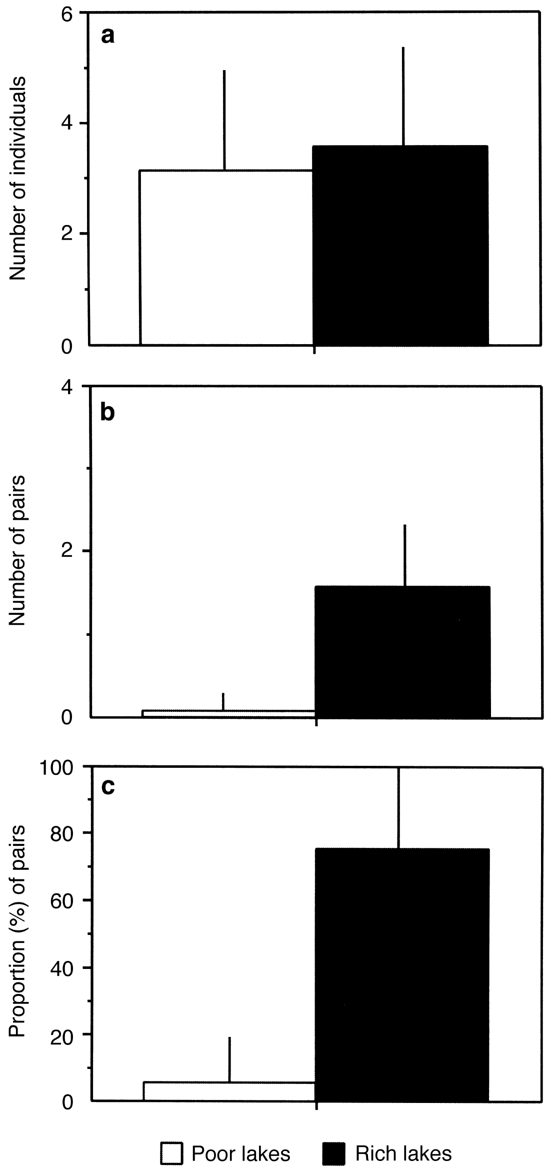

Fig. 1. Means (+ 1 SD) of (**a**) total number of individuals, (**b**) number of pairs, and (**c**) proportion of paired individuals of introduced mallards in poor lakes (n = 6) and rich lakes (n = 6), respectively. Six mallards (3 males, 3 females) were introduced to each lake; hence maximum values were six for number of individuals and three for pairs. See material and methods for further explanation.

Results

The mean total number of observed introduced mallards per census did not differ between poor and rich lakes (Fig. 1a; U = 22.5, p = 0.92). By contrast, the mean number of pairs and, consequently, the proportion of paired individuals were higher on rich lakes than on poor (Fig. 1b and c; number of pairs, $U = 35.5$, $p = 0.008$; proportion of paired individuals, $U = 35.5$, $p = 0.008$). Generally speaking, introduced mallards formed separate pairs on lakes that were, in a relative sense, high-quality brood habitats, whereas they did not on lakes of low-quality brood habitat.

Discussion

Because pair formation of wild mallards normally takes place on wintering grounds (McKinney 1986, Bluhm 1988), it is clear that the pair formation of the introduced birds in our experiment does not fully reflect a natural situation. Nor do we claim that courtship and mate choice (e.g. Holmberg *et al.* 1989) in our wing-clipped birds in all details followed their normal behavioural routes. However, because renesting is frequent in mallards, pair formation involving mate switching also occurs in the breeding season (McKinney 1986 and references therein). Furthermore, unpaired males may frequently try to form pair-ponds during the breeding season (McKinney *et al.* 1983, Goodburn 1984). Therefore, we consider the pair formation among the introduced birds as a biologically reasonable measure of mallards preparing for breeding.

Our results give further support for the role of habitat quality, especially food limitation at the brood stage, in individual and population level processes in breeding mallards. The absence of pair formation among the introduced birds on poor lakes suggests that, if food requirements at the brood stage are not met, a lake may not induce visiting birds to prepare for nesting, but it will rather remain without nesting pairs. We showed previously that the food resource level at the time of selecting a nesting lake can be used to predict the resource level at the brood stage (Pöysä *et al.* 2000). The present results agree with our earlier finding that a considerable proportion of seemingly suitable lakes on a landscape may remain unoccupied by nesting individuals (Pöysä *et al.* 1998, 2000, Sjöberg *et al.* 2000).

Our present and earlier results for mallards have direct ties to the current approach of using individual behaviour in studying population level phenomena and conservation problems (e.g. O'Connor 1985, Sutherland 1996, Fryxell & Lundberg 1997, Caro 1998, Sutherland 1998a, Reed 1999). This approach is especially timely and relevant for studies dealing with habitat-related problems, because habitat deterioration and loss are considered to be major global threats to migratory bird populations, including Anatidae (e.g. Green 1996, Sutherland 1998b). The black duck *Anas rubripes*, ecologically very similar to the mallard, is one good example (Dwyer & Baldassarre 1994). We suggest that behavioural and other individual level aspects studied by us with respect to habitat quality, especially pair formation among introduced birds (this study), as well as response of imprinted ducklings to habitat quality (Nummi *et al.* 2000, Sjöberg *et al.* 2000; *see also* Pöysä *et al.* 2000) provide a tool for assessing the quality of wetland habitats.

At this point it may appear tempting to use a surrogate, like the concentration of total P in the water, as a convenient shortcut to measure a lake's suitability as a brood rearing habitat (Kerekes *et al.* 1990, Staicer *et al.* 1994, Sjöberg *et al.* 2000). However, we advise against this. Although lakes with mallard pairs and broods generally have relatively high P concentrations, the opposite may not always be the case. That is, high productivity may manifest itself in high fish biomass rather than ducks. Therefore, using the mallards themselves to measure habitat quality should be a more reliable method. For example, our experimental procedures could be used in assessing *a priori* the suitability of man-made and natural habitats for the management of mallard and other wildfowl populations (Street 1977, The Game Conservancy 1993). In this way wildfowl release and habitat restoration programmes (e.g. Myrberget 1990, The Game Conservancy 1993, Callaghan & Kirby 1996) could be directed to profitable sites and wasting of limited resources avoided.

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