

NOTE BRÈVE

EFFECTS OF PREMIGRATORY FASTING ON THE POTENTIAL FOR LONG DISTANCE DISPERSAL OF SEEDS BY WATERFOWL: AN EXPERIMENT WITH MARBLED TEAL

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RÉSUMÉ. — *Effets du jeûne prémigratoire sur la potentialité des oiseaux d'eau à disséminer des graines à longue distance : une expérience avec la Sarcelle marbrée.* — L'effet possible du jeûne prémigratoire sur la potentialité des oiseaux migrateurs à disséminer au loin des graines a été testé en captivité sur neuf Sarcelles marbrées *Marmaronetta angustirostris*. En début d'expérience les oiseaux ont été gavés avec un mélange de graines de deux espèces de *Scirpus* (dont une avec de grosses graines) et de marqueurs en plastique de deux tailles différentes (\varnothing 1,0 et 0,5 mm). Cinq individus ont été privés de nourriture durant 8 heures (phase de jeûne) puis privés à la fois d'eau et de nourriture durant 8 autres heures (phase de simulation de vol). Quatre individus de contrôle ont subi la phase de vol mais sans jeûne préalable. Plus de 16 heures après le gavage, un nombre significatif de graines et de marqueurs de petite taille fut recueilli dans les fèces alors que les graines et les marqueurs de grande taille en étaient pratiquement absents. Quand la nourriture fut de nouveau mise à disposition après la phase de simulation de vol, les oiseaux qui avaient été auparavant soumis à une phase de jeûne déféquèrent plus de graines de la petite espèce et de petits marqueurs que les individus de contrôle. Ces résultats suggèrent que le jeûne prémigratoire peut favoriser la dispersion à longue distance de graines par les oiseaux via la rétention de propagules dans le tube digestif.

Many aquatic plants and invertebrates lack the capacity to colonize new areas by themselves, but it is striking how they often occupy wide geographic ranges (Good, 1953; Raven, 1963). Waterfowl (ducks, geese and swans) have been proposed as important agents for the dispersal of aquatic organisms by transporting the propagules adhered to their body, or internally in the digestive tube (Darwin, 1859; Ridley, 1930). This idea appeared a long time ago in the literature, yet little information is available on the true role of waterfowl as dispersors of aquatic organisms (but see Figuerola & Green, 2002, 2003; Green *et al.*, 2002). For successful long-distance internal dispersal by waterfowl to occur we can identify three essential steps: 1) birds ingest the propagules, 2) the propagules are retained long enough inside the duck to allow the arrival of the birds to new areas, and 3) the propagules survive digestion and find the conditions necessary for establishment in these new areas (Charalambidou *et al.*, 2002; Clausen *et al.*, 2002; Green *et al.*, 2002).

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Evidence in support of the accomplishment of these three stages has been provided in laboratory and field studies (see review in Figuerola & Green, 2002). However, several questions remain uninvestigated. Some authors have suggested that birds may empty their guts prior to the start of migration (Morton, 1967). The period of migratory fasting and the reduction in the size of digestive organs reported in several different bird species gives support to this hypothesis, at least for some grebes, waders and passerines (see Jehl, 1997; Fransson, 1998; Piersma & Drent, 2003), although other studies have not found evidence of reduced feeding prior to the start of migration (passerines, Carpenter *et al.*, 1983; Lindström & Alerstam, 1992; Bewick's swans, Clausen *et al.*, 2002). Although experiments in captivity have shown that seeds can be retained in waterbirds for periods of more than 24 hours (Figuerola & Green, 2002), it is currently unclear whether, under field conditions, any seeds will remain in the gut to be dispersed if birds initiate a period of fasting prior to the migratory flight.

To assess the impact of premigratory fasting on the potential for long distance seed dispersal by waterfowl, we report here on an experiment performed under controlled conditions in captivity.

METHODS

The experiment was performed at the Wildlife Recovery Centre in Doñana National Park on Marbled Teal (*Marmaronetta angustirostris*), a duck species that makes extensive migratory and dispersive movements within its range (Green, 1993; Navarro & Robledano, 1995), and known to ingest and defecate large numbers of apparently viable seeds of aquatic plants (Figuerola *et al.*, 2002, 2003; Green *et al.*, 2002). Nine captive bred Marbled Teals were individually housed in cages (three meters long by three meters wide), with wire mesh covering the sides and roof. The floor of each cage was occupied by a rectangular concrete pond which was surrounded by a band of soil (approximately 0.5 meter wide) covered with a layer of fine sand. Prior to the start of the experiment, the ponds were emptied, allowed to dry and the drainage pipe was sealed with plastic bags and adhesive tape. Two of the cages lacked a concrete pond, having a soil floor covered with fine sand. The birds, previously housed together in a different cage, were redistributed individually in each of the cages the night before the start of the experiment (18 October 1999). Water and food (commercial duck-food pellets) were provided *ad libitum* on separate dishes.

The next morning a mixture of 100 seeds of *Scirpus maritimus*, 100 seeds of *Scirpus litoralis*, 60 plastic markers of 1.0 mm diameter and 100 plastic markers of 0.5 mm diameter were force-fed to each individual duck. Seeds were collected from brackish marshes in Doñana Natural Park, and are major food items of the Marbled Teal in the Mediterranean region (Green & Selva, 2004; Fuentes *et al.*, 2004). Seeds of both species can retain their viability after digestion by Marbled Teal (J. Figuerola, A.J. Green & L. Santamaría, unpublished data). While the provision of food and water was constant for four control individuals, food was removed from the cages of the five experimental individuals to simulate a period of fasting before the start of migration. After eight hours, food (for control birds) and water supply (for both control and experimental birds) were removed to simulate a period of no availability of food and water during a nocturnal migratory flight. After another eight hours (i.e. 16 hours following the ingestion of the seeds), both food (pellets) and water supply were returned. Droppings were collected after two hours, four hours and then at four hour intervals up to 16 hours after the start of the experiment. Unfortunately, a rain storm started approx. 19 hours after ingestion of the seeds, washing away part of the droppings produced in the 16-25 hour interval. A final collection of droppings was conducted 32 hours after the start of the experiment. This last collection included part of the droppings produced in the 16-25 hour interval (those not washed away by the rain) and all the droppings produced from 25 to 32 hours. Given that treatment and control birds were randomly distributed across the installations, rain could not be expected to affect the comparison between treatments. Since part of the droppings produced (and consequently, part of the defaecated seeds and markers) were washed away by the rain, we did not analyse the total proportions of seeds and markers recovered throughout the experiment. Instead, we compared the absolute number of the different seeds and markers recovered in each phase of the experiment by using Wilcoxon rank sum tests. Individual ducks were taken as the unit for analysis in all the statistical tests.

RESULTS

The experiment can be divided into three phases: the treatment phase (with access to water in the first eight hours for experimental birds, and access to food and water for control birds), the flight simulation phase (without access to food or water during the 8-16 hours period) and a final refuelling phase (16-32 hours). The seeds of the larger species (*S. maritimus*) and the larger size of the markers (1 mm \varnothing) were hardly represented in fae-

ces in the last period of the experiment (> 16 hours). Only eight *S. maritimus* seeds and one 1 mm marker were recovered from a single duck during the 16-32 hours period. Given their anecdotal presence in the droppings in the last phase of the experiment, no statistical analyses were performed for these two seed/marker types (Fig. 1).

No significant differences in the number of the smaller seeds (*S. litoralis*) or markers (0.5 mm \varnothing) were observed between experimental and control birds during the treatment period (i.e. first eight hours) of the experiment (markers, $z = 0.86$, $P = 0.39$, *S. litoralis*, $z = 0.61$, $P = 0.54$, Fig. 2). During the flight simulation phase, controls defaecated significantly more *S. litoralis* seeds than experimental birds ($z = 2.05$, $P = 0.04$), but no differences occurred for the number of markers in the droppings ($z = 0.13$, $P = 0.89$). During the refuelling phase (16-32 hours), the droppings collected from experimental birds contained significantly more markers ($z = 2.02$, $P = 0.04$) and *S. litoralis* seeds ($z = 2.05$, $P = 0.04$) than droppings from control individuals (Fig. 2).

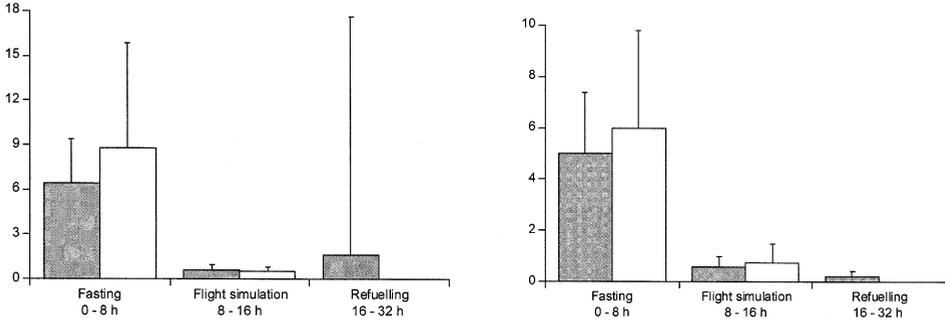


Figure 1. — Number (mean \pm SE) of (a, left) *Scirpus maritimus* seeds and (b, right) 1.0 mm \varnothing markers found in the droppings collected from five experimental and four control Marbled Teal during the three phases of the experiment. ■ experimental ducks □ control ducks (not subjected to the first 8 h fasting period).

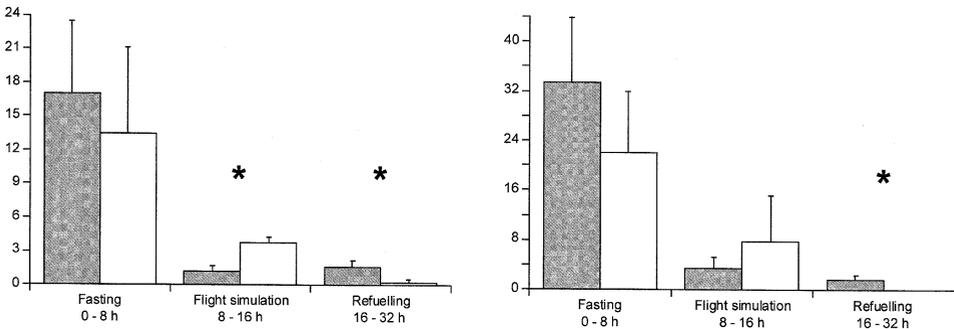


Figure 2. — Number (mean \pm SE) of (a, left) *Scirpus litoralis* seeds and (b, right) 0.5 mm \varnothing markers found in the droppings collected from five experimental and four control Marbled Teas during the three phases of the experiment. * Indicates a significant difference ($P < 0.05$) between control (not subjected to the first 8 h fasting period) and experimental birds. ■ experimental ducks □ control ducks.

DISCUSSION

An increasing number of studies are reporting short-term morphological changes in birds during migration (also known as phenotypic flexibility, Piersma & Lindström, 1997; Piersma, 1998). Field data indicate that, during migration, individuals seem to reduce the size of their digestive organs (gizzards, livers, kidneys and guts) and increase their fat depo-

sits (i.e Piersma & Gill, 1998; see also Gauthier *et al.*, 1984). Experiments in captivity have concluded that changes in digestive organs in birds during migration are similar to those experienced by individuals exposed to short periods of fasting (Biebach, 1998). Such a reduction in the activity of digestive organs can have opposing consequences for the probability of dispersal of propagules by waterfowl. On the one hand, the number of propagules retained in the digestive tube may be reduced, since most of the tube is probably emptied before the start of migration. On the other hand, this reduction in digestive activity may allow very long retention times for any propagules remaining inside the birds.

In our experiment, both control and experimental birds defaecated fewer seeds and markers of the larger size during the last phase of the experiment (when long distance dispersal would be likely to occur) when compared with small seeds and markers. We suggest this size effect can be explained by the negative relationship between seed size and retention time in the digestive tube already reported in cedar waxwings (Levey & Grajal, 1991). Larger seeds may also be less resistant to digestion by ducks (De Vlaming & Proctor, 1968), leaving fewer viable seeds to be defaecated. However, large markers (1.0 mm Ø) were also retained for shorter periods than smaller ones (0.5 mm Ø), suggesting that seed size is an important variable affecting retention time, seed shadows and the potential for endozoochorous dispersal.

In our experiment, we explored the potential effects of premigratory fasting on seed dispersal by ducks. Our results indicate that, although fasting individuals defaecated a large number of seeds in the first few hours after feeding, they retained *S. littoralis* seeds for a longer period than control individuals. Thus, premigratory fasting may increase the potential for long distance dispersal of propagules by increasing the number of seeds retained for a long time (more than a day) at the potential cost of a reduction in the number of seeds retained for intermediate periods of time (8-16 hours). Clearly, a period of fasting prior to the start of migration should not be considered an unassailable barrier for the occurrence of bird mediated long distance dispersal, contrary to previous suggestions (Clausen *et al.*, 2002).

Although the conditions in captivity may have affected the outcome of the experiment, we suspect our results underestimate the potential for dispersal in the field. Birds in captivity have shorter ceca and intestines (Clench & Mathias, 1995; Liukkonen *et al.*, 2000), a change likely to accelerate the passage rate of seeds (Karasov, 1990; Jordano, 1992; Traveset, 1998). We expect that this reduction in gut size and consequent acceleration of passage time acted to reduce the number of seeds retained for longer periods inside guts of the captive Marbled Teals. While the conditions of our experiment represent a crude approximation to conditions experienced by birds in the field, we suggest that our experiment provides relevant information on the qualitative effects of premigratory fasting on the potential for dispersal of aquatic organisms.

More research is needed to study the effects of fasting over longer periods of time (> 16 hours), to investigate the effects of fasting on the viability of seeds following passage through the gut, and to determine the occurrence and extent of migratory fasting in ducks under field conditions.

Our experiment provides further evidence that migratory waterfowl play a major role in the long-distance dispersal of aquatic plants (see also Green *et al.*, 2002; Figuerola *et al.*, 2002, 2003). Marbled Teals make regular movements between wetlands such as Doñana and El Hondo in Spain, and Sidi Moussa in Morocco (Green, 1993; Navarro & Robledano, 1995), all sites holding *S. littoralis* and *S. maritimus* and separated by more than 500 km from each other. Based on this experiment and other field data on diet (Fuentes *et al.*, 2004), we expect that teals move viable *Scirpus* seeds between such wetlands.

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