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Commensal foraging with Bewick's Swans *Cygnus bewickii* doubles instantaneous intake rate of Common Pochards *Aythya ferina*

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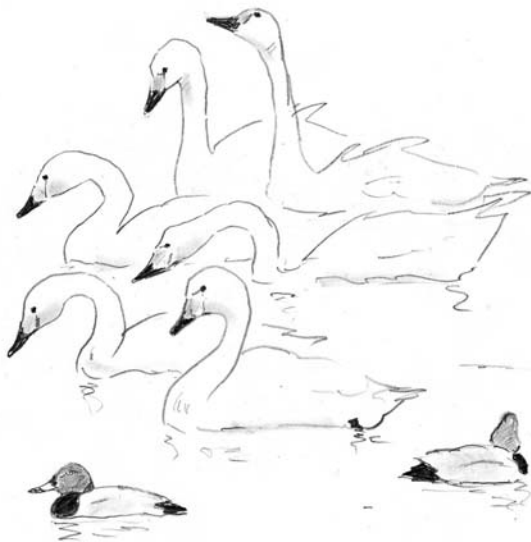
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Aquatically foraging Bewick's Swans *Cygnus bewickii* have been repeatedly reported to be accompanied by diving ducks, but the exact nature of this relationship is unclear. Based on field observations, we found a strong correlation between the number of foraging swans and the number of foraging Common Pochards *Aythya ferina* and Tufted Ducks *Aythya fuligula* at our study site (Lauwersmeer, the Netherlands), with the median ratio being close to one diving duck per swan. To determine whether the association was kleptoparasitic or commensal, we measured in a series of experimental trials the instantaneous intake rates of Bewick's Swans and Common Pochards when foraging alone and when foraging together. On average, pochards in company with a swan attained twice the instantaneous intake rate as compared with foraging alone. This was mainly due to gleaning food items that floated away as a result of the swan's trampling activity, and was not due to stealing: in fact, food intake rates of swans were not affected by the presence of a pochard.

Key words: co-occurrence, foraging, tundra swan, pochard, diving duck, kleptoparasitism, commensalism, facilitation, depletion

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Birds commonly forage in mixed-species flocks (Sridhar *et al.* 2009). The relationship in such associations may be kleptoparasitic, where one species is stealing food from another (e.g. Ens & Goss-Custard 1984, Percival & Evans 1997, Dubois & Giraldeau 2005). However, associative foraging does not necessarily have to be negative for either of the species. Mixed-species groups are, for instance, more likely to detect and avoid predators, to the mutual benefit of both species (Dickman 1992, Beauchamp 1999, Goodale & Kotagama 2008). In other cases, the relationship is commensalistic, with one species benefitting from the association while the other species remains unaffected, for instance when food (of no interest to the other species) becomes available for one species due to the foraging activities of the other species (Hino 1998, Dijkse & Ouweneel 2005, Källander 2005). To understand why species forage together, information on the costs and benefits of the

association is needed. However, such measurements have rarely been carried out under controlled conditions (but for field experiments see Hino 1998, Stienen & Brenninkmeijer 1999).

Bewick's Swans *Cygnus bewickii*, as well as the closely related Whooper Swans *Cygnus cygnus* and Whistling Swans *Cygnus columbianus*, are often observed foraging together with dabbling and diving ducks (Sherwood 1960, Bailey & Batt 1974, Beekman *et al.* 1991, Nolet *et al.* 2002, Källander 2005). At one particular site Källander (2005) compared how 41% of the Whooper Swans and 51% of the Bewick's Swans were accompanied by several duck species and Eurasian Coots *Fulica atra*, whereas only 2.6% of the Mute Swans *Cygnus olor* were followed by waterfowl. Swan species that trample in the water to excavate food from the sediment (a common foraging technique of Bewick's, Whooper and Whistling Swans and to a

lesser extent of Mute Swans) may destroy important food sources of ducks (see Sherwood 1960, Petrie *et al.* 2002 and references within), but ducks might on the other hand profit from the swans' foraging technique, as it could enhance the availability of their food (Sherwood 1960, Källander 2005). Ducks have even been suggested to kleptoparasitize swans by stealing tubers (Beekman *et al.* 1991).

In order to clarify the relationship between diving ducks and aquatically foraging Bewick's Swans, we carried out an experiment under controlled conditions, designed to explore whether the observed association in the field is kleptoparasitic, mutualistic or commensalistic. We did this by quantifying instantaneous intake rates of the two species while foraging alone and together. We expected that the instantaneous intake rate of diving ducks would be higher in the presence of swans than when foraging alone, while we expected the reverse for the swans, i.e. a kleptoparasitic relationship as described by Beekman *et al.* (1991).

METHODS

Field data

Bewick's Swans use the Lauwersmeer (53°22'N, 06°13'E) in the Netherlands as their last stopover site on autumn migration, and commonly spend several weeks there in October – November (Beekman *et al.* 1991, Gyimesi *et al.* 2012). The >2000 ha lake has nine creeks where the water is shallow enough for swans to reach the bottom. The submerged vegetation in these parts is dominated by Fennel Pondweed *Potamogeton pectinatus*, which produces tubers, asexual reproduction organs that overwinter in the sediment, whereas the aboveground parts of the plant die off in late summer (Pot 1984, van Wijk 1988, Hidding *et al.* 2010). Bewick's Swans are known to forage exclusively on these tubers during their stay at the Lauwersmeer, commonly being accompanied by diving ducks *Aythya* spp. (Beekman *et al.* 1991, Nolet *et al.* 2002). By trampling in the water, the swans whirl up sediment and tubers, and thus create a foraging pit (Brouwer & Tinbergen 1939). The heavier sediment particles settle more quickly in the pit than the tubers, which subsequently become accumulated on top, especially at the edges of the pit (van Eerden *et al.* 1997).

In order to determine whether within-season fluctuations in swan numbers are followed by duck numbers, field counts were carried out in 1995 in one of the creeks. On eight days, the Bewick's Swans and diving ducks foraging within the swan flocks were recorded at

hourly intervals. The average numbers of swans and ducks per day were natural log-transformed to reach normality and subsequently correlated.

In addition, to confirm the association between seasons, we counted foraging swans and ducks once a day in four creeks during three consecutive years. On average, we carried out the counts on 7.4 (± 3.9 SD), 12.5 (± 4.7) and 5.0 (± 5.0) days per creek, in 2005, 2006 and 2007 respectively. We calculated the median duck/swan ratio for 1995 and tested whether it was significantly different from the mean of the 2005–2007 ratios (normally distributed data) in a one-sample *t*-test. For 2005–2007, the effect of swan numbers on diving duck numbers and in interaction with the random factors year and creek was tested by a GLM analysis (type III decomposition).

Experiment

Bewick's Swans create pits of approximately 1 m² in the sediment (van Eerden *et al.* 1997, Klaassen *et al.* 2006). In order to simulate such a feeding pit, we used a 1 × 1 m metal tray (with 0.1 m high sides), filled with sand and placed at the bottom in the middle of an experimental arena (3 × 6 m) of a concrete basin (Figure 1). Wheat grains were homogeneously spread in the tray, and covered with 0.05 m of sand. The sand was tamped down for higher compaction, and the water depth was set at 0.45 m above the top of the tray, a common foraging depth of swans in the field (Nolet *et al.* 2006a). Trials were carried out using four food densities simulating those naturally occurring (i.e. 16 g, 30 g, 52 g, and 74 g/m² fresh weight). Water saturated wheat grains are similar to pondweed tubers in nutrient composition and size, and have successfully been used in earlier foraging experiments to replace tubers (Nolet *et al.* 2001, Nolet *et al.* 2006a). The experiment was conducted during February – April, 2008.

Four Common Pochards (two males and two females) and four Bewick's Swans (two males and two females) took part in the experiment (all birds > one year old). Birds were fitted with leg rings for individual recognition. All birds had been raised in captivity, except for one wild-caught swan that had been in captivity for more than five years. The basin and its surroundings had formed the standard housing for more than a year prior to the experiment.

To familiarize the birds with the experimental facilities and procedure, they were trained for five weeks prior to the experiment. At the end of this period, they started foraging as soon as they entered the experimental area and exhibited natural foraging behaviour during the trials. The birds not involved in a trial were

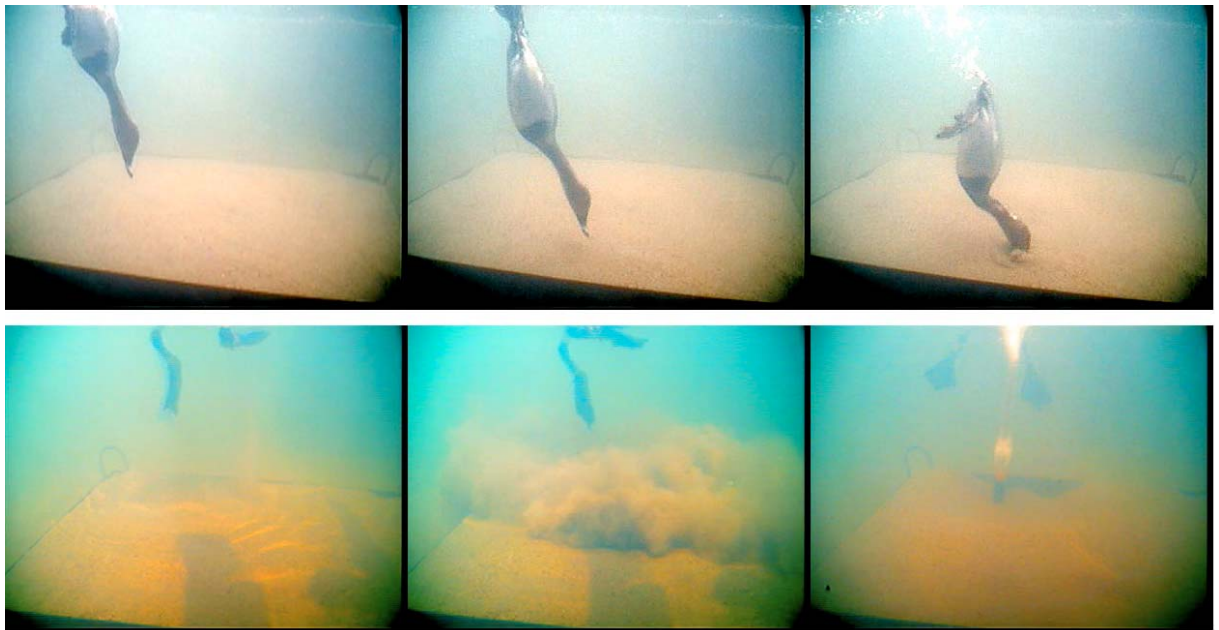


Figure 1. Upper pictures: Pochard descending from the surface (left) to forage by filter-feeding in the experimental tray (right). Lower pictures: Bewick's Swan starts to trample above the experimental tray (left) and by whirling up the sediment (middle) creates a pit to forage from by head-dipping (right). Images recorded from the video files.

kept in the surroundings of the basin allowing visual and audible contact between all birds. In order to keep the birds motivated to forage during the trials in the morning hours, food access outside the trials was limited to the afternoons (between 13:00 and 17:00 hours).

All individuals were used in a 'combined' trial (a swan and a pochard together), and in a 'solitary' trial (a swan or a pochard alone) at each of the four food densities. This resulted in 48 trials (4 individuals \times 3 species treatments \times 4 food densities). Food depletion can severely influence instantaneous intake rates (Royama 1971, Sutherland & Allport 1994, Wanink & Zwarts 2001), and thus experiments intending to measure individual intake rates of several animals foraging together need to take this into account. Based on preliminary measurements during the training trials, we assumed the intake rate of Bewick's Swans to be approximately three times that of pochards. Therefore, the duration of solitary swan trials was set to a third of that of solitary pochard trials (120 s and 360 s, respectively, measured as cumulative feeding time during the trials). Combined trials were terminated on reaching 90 s swan cumulative feeding time (encompassing about 90 s of cumulative feeding time of the accompanying pochard, assumed to be equivalent to 30 s of swan cumulative feeding time). We expected that these three treatments would all result in a roughly equivalent

depletion, so that any observed intake rate differences among treatments would not be the result of differences in the level of depletion.

All trials took place between 8:30 and 13:00. We carried out two to four trials per day. Individuals were randomly assigned to treatments, with the restriction that a given individual was only tested once per day. The trials were filmed above and under water by a Panasonic NV-GS15 camera and analysed using the software Pinnacle studio v70205. Feeding times of pochards (time spent under water) in the combined trials and trampling times of swans (foot movements under water with the head above water) were measured from the videos.

After each trial, the sediment was pumped through a sieve with 3 mm mesh size to collect the wheat grains left behind. Seeds inside and outside the tray were kept separately. The collected seeds were dried for 48 h at 60°C to obtain their dry weight (on average $88.7 \pm 1.0\%$ of fresh weight; all further weights refer to dry weights). Parallel to a trial, the same weight of seeds as offered in the trial received a control treatment (i.e. kept in water and later dried together with the seeds collected after the trial). The total amount of seeds consumed (C) was determined by subtracting the weight of the collected seeds from the weight of the control seeds. Instantaneous intake rates (I_i) in the

solitary trials were calculated as

$$I_i = C / T_f,$$

where T_f is cumulative feeding time.

For the combined trials, the calculations of instantaneous intake rates relied on the assumption that pochards were only foraging outside the tray, and swans only inside it, both based on the analysis of the video images. The total amount of seeds spread outside the tray was estimated from the regression with the trampling time of swans (see Results for the equation). The seed consumption by pochards (C_p) was calculated as

$$C_p = N_{out,e} - N_{out,m},$$

where $N_{out,e}$ is the estimated amount of seeds outside the tray based on swan trampling time and $N_{out,m}$ is the measured amount of seeds outside the tray. Pochard instantaneous intake rates (I_{ip}) were calculated as

$$I_{ip} = C_p / T_{fp},$$

where T_{fp} is the cumulative feeding time of pochards. Subsequently, swan intake rates (I_{is}) were calculated as

$$I_{is} = (C - C_p) / T_{fs},$$

where T_{fs} is the cumulative feeding time of swans.

All measured seed weights needed log-transformation to reach normal distribution. Comparisons between solitary swan trials and combined trials with respect to trampling times, amount of seeds inside and outside the tray, as well as intake rates were carried out with GLM analyses with the fixed factors treatment type and food density, and individual as a random factor. The interaction of treatment type with individual was left out of the model due to the lack of replicates. The other interactions were removed from the final models due to not being significant. In order to compare the proportion of trampling time of individual swans at corresponding food densities between a solitary swan trial and a combined trial, arcsine-transformed proportions were compared by paired t -tests.

RESULTS

Field data

Within season, the temporal peaks in foraging Bewick's Swan numbers were closely tracked by peaks in foraging diving duck numbers (Figure 2). Numbers of

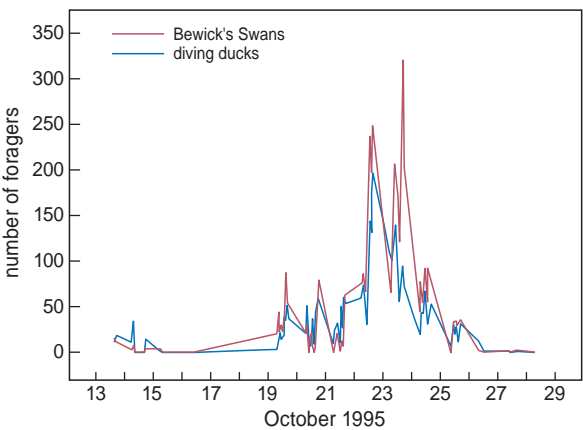


Figure 2. Number of foraging Bewick's Swans and diving ducks (Common Pochards and Tufted Ducks) counted at hourly intervals in a single creek in autumn 1995.

Common Pochards and Tufted Ducks each showed a significant correlation with swan numbers ($r^2 = 0.78$, $P < 0.0001$ and $r^2 = 0.55$, $P < 0.0001$, respectively), but summing their numbers slightly increased the strength of the correlation ($r^2 = 0.81$, $P < 0.0001$). Based on 43 hourly scans, the mean number of foraging diving ducks per foraging swan was 3.43, with a median of 1.41 (data was heavily skewed: Shapiro-Wilk test = 0.69; $P < 0.001$).

Based on the data collected in the period 2005–2007 in four different creeks, the positive correlation between foraging Bewick's Swans and foraging diving ducks also existed throughout years at the whole study site (Table 1). The mean of the duck/swan ratios observed in this period was not significantly different from the median of the 1995 data ($t_{69} = -0.3$; $P > 0.7$). However, the GLM analysis revealed that besides the main effect of swan numbers on duck numbers, the

Table 1. The effect of foraging Bewick's Swan numbers, as well as the random factors year and creek and their interactions on numbers of foraging diving ducks in 2005–2007.

	Sum of squares	Df	F	P
Intercept	0.49	1	0.13	0.76
Year	10.24	2	1.77	0.18
Creek	7.71	5	0.53	0.75
Swan nr	375.69	1	15.33	<0.05
Creek × Swan nr	42.37	5	2.93	<0.02
Year × Swan nr	52.87	2	9.13	<0.001
Error	280.71	97		

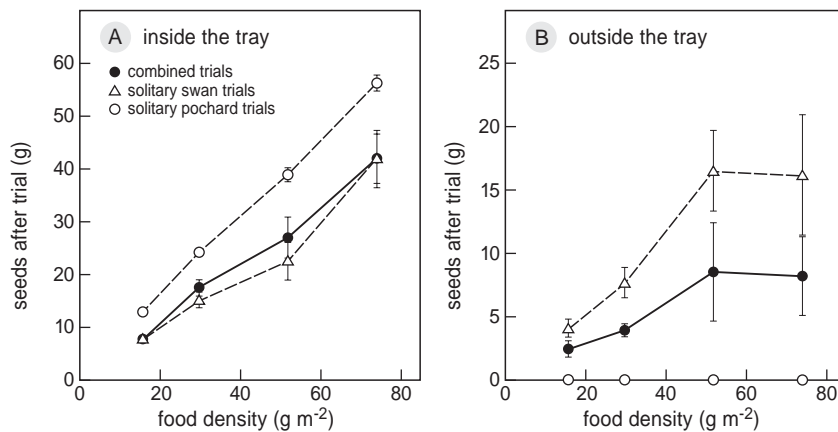


Figure 3. Amount of seeds collected inside (A) or outside (B) the tray after trials with a swan foraging either without ('solitary swan trial') or with a pochard ('combined trial') at four food densities. For comparison, trials with a pochard foraging alone ('solitary pochard trials') are also presented with open circles (no seeds found outside the tray in these trials). Note the different ranges on the y-axes of the two panels. Means \pm standard errors are given.

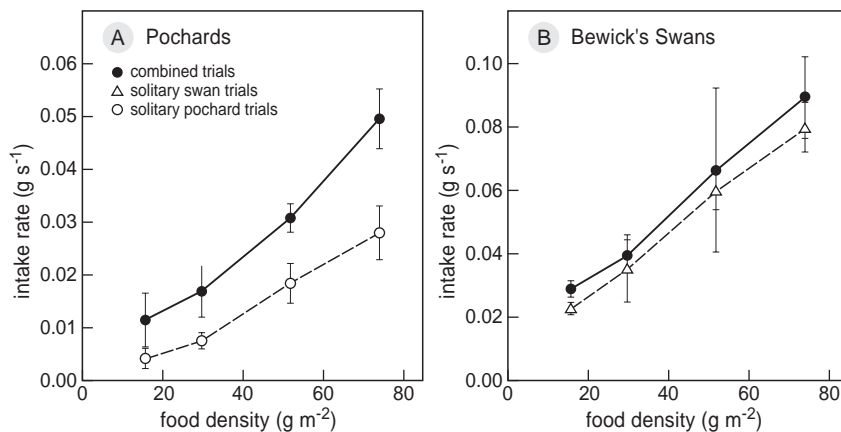


Figure 4. Calculated instantaneous intake rates of pochards (A) and swans (B) when foraging alone ('solitary trials') or accompanied by the other species ('combined trials'). See text for the calculation. Given are means \pm standard errors. Note the different scale ranges on the y-axes.

interactions with creek and year were also significant (Table 1). In other words, the number of diving ducks following one swan was not the same in each creek and in each year.

Experiment

During the solitary trials, swans and pochards fed from the tray only. The underwater video recordings revealed that pochards ploughed through the sediment with their bill, searching for seeds by touch. In contrast, after trampling, Bewick's Swans consumed seeds accumulated at the sediment surface in their foraging pit, by sucking up water together with the seeds. Swans were also feeding from the tray during the combined

trials, but the pochards kept some distance from the swans and collected the seeds outside the tray spread by the swans' trampling. We witnessed a pochard searching in the tray simultaneously with a swan only on one occasion.

Considering the solitary swan trials, the amount of seeds found outside the tray ($N_{out,e}$) strongly correlated with total trampling time (T_t), increasing with time spent trampling ($N_{out,e} = \exp(1.09 + 0.04 \times T_t)$; $F_{1,15} = 9.51$, $P < 0.01$). Trampling times did not differ significantly between the solitary swan trials and the combined trials ($F_{1,26} = 1.06$, $P > 0.3$). Although the absolute amount of trampling did not differ, this meant that the proportion of time spent trampling was higher

during the shorter combined trials ($t_{15} = 2.3$, $P < 0.05$). Nevertheless, based on the similar absolute trampling times, a similar amount of seeds was expected outside the tray in solitary and combined trials. However, the amount of seeds found *outside the tray* was lower in the combined trials than in the solitary swan trials ($F_{1,26} = 22.93$, $P < 0.001$; Figure 3). In contrast, the amount of seeds remaining *inside the tray* showed no difference between the combined trials and the solitary swan trials ($F_{1,26} = 2.74$, $P > 0.1$; Figure 3).

Pochards on average doubled their instantaneous intake rate relative to when foraging alone ($F_{1,26} = 15.33$, $P < 0.001$; Figure 4), whereas intake rates of swans did not significantly differ ($F_{1,26} = 3.71$, $P > 0.06$; Figure 4).

DISCUSSION

Our field study showed that diving ducks were closely associated with aquatically foraging Bewick's Swans. Our experimental results suggest that diving ducks benefit energetically from this association: when foraging with a swan, pochards attained instantaneous intake rates on average twice as high as when foraging alone, by feeding on the food items drifting away from the swans. In contrast, swan intake rates were not directly affected by the association, because ducks did not feed in the foraging pits. Therefore, considering instantaneous intake rates, the relationship should be regarded as commensal, against our expectations, with pochards profiting and swans not being negatively affected.

The strong fluctuations in foraging Bewick's Swan numbers were caused by swans switching between foraging and sleeping (Nolet & Klaassen 2005), as well as by arriving at or leaving the stopover site on their migration (Nolet *et al.* 2002). The hourly scans may have been affected by temporal autocorrelation, but the daily counts throughout three years confirm that the association between Bewick's Swans and diving ducks is a regular phenomenon at our site (Beekman *et al.* 1991, Nolet *et al.* 2002). The significant interaction terms between swan numbers with year and creek suggest that the number of ducks following one swan is influenced by local and temporal conditions, such as food densities or flock size of swans.

Thanks to their special foraging technique, Bewick's Swans can accumulate a high food density in their pit. As a result, they can probably reach much higher intake rates than by simple filter-feeding. In contrast, the food drifting away during trampling is spread out over a

large area, forming a much lower density than in the foraging pit. Therefore, it is probably not profitable for swans to search for these food items. The lower amount of seeds found outside the tray after the combined trials compared with the solitary swan trials reflect food consumption by the pochards *outside the tray*. The giving-up density (i.e. the amount of food left behind) of diving ducks might be much lower than that of Bewick's Swans (i.e. on average 3.6 g/m^2 in the closely related Canvasbacks *Aythya valisineria* foraging on tubers of *Vallisneria americana* (Lovvorn & Gillingham 1996) against a lowest observed average of 14.5 g/m^2 of Bewick's Swans foraging on pondweed tubers at the Lauwersmeer (Nolet *et al.* 2001)). In other words, ducks consider lower densities still worth to feed, and thus probably also the food items drifting away from swans. In fact, the results of our experiment suggest that by switching from filter-feeding to collecting food from the sediment surface, ducks can considerably increase their instantaneous intake rates.

One may argue that testing intake rates on one food patch does not reflect natural circumstances. However, detailed field measurements revealed that the average foraging time of Bewick's Swans per foraging pit is 273 s (Nolet *et al.* 2006b), while they make only short movements ($< 1 \text{ m}$) above their foraging pits (Klaassen *et al.* 2006). Therefore, our experimental swan trials were kept short, and the swans also foraged only from the tray. The food spreading out from the tray settled at the bottom of the basin together with some sand, and thus created a semi-natural foraging surface for the ducks.

All in all, although experimentally created conditions can never fully replace natural conditions, we believe that the behaviour observed in the experiment also applies to the field situation. Moreover, even if the actual instantaneous intake rates in the field are unlike those observed in our experiment, the intake rate differences that we found in pochards were large. In fact, the pochards' instantaneous intake rate increased so much that while in solitary trials they collected only a third as much food as a swan per time unit (corresponding to our assumptions), in combined trials they attained intake rates at the higher food densities that were in the range of those of the swans. Nevertheless, pochards consumed seeds only outside the tray, and thus did not cause additional depletion inside it. Therefore, in hindsight, combined trial durations could have been made equal to those in solitary swan trials.

Based exclusively on field observations, it is difficult to judge whether the relationship between diving ducks and Bewick's Swans is kleptoparasitic or commensal-

istic (Beekman *et al.* 1991, Källander 2005). Our experimental results revealed that pochards have no immediate negative effects on Bewick's Swans, while they profit themselves from the association. However, in the long run food might be depleted more rapidly due to the elevated consumption rate of ducks, which might limit the period that Bewick's Swans can make use of a stopover site during migration, and thus generate a form of delayed kleptoparasitism. This scenario could only occur if pochards keep their daily foraging times as when foraging without swans, and do not quit foraging earlier due to saturation. Therefore, future studies should quantify the long-term intake rate Common Pochards can reach in the field, and how that affects the carrying capacity of a stopover site for Bewick's Swans.

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REFERENCES

- Bailey R.O. & Batt B.D.J. 1974. Hierarchy of waterfowl feeding with Whistling Swans. *Auk* 91: 488–493.
- Beauchamp G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behav. Ecol.* 10: 675–687.
- Beekman J.H., van Eerden M.R. & Dirksen S. 1991. Bewick's Swans *Cygnus columbianus bewickii* utilising the changing resource of *Potamogeton pectinatus* during autumn in the Netherlands. *Wildfowl Supplement* 1: 238–248.
- Brouwer G.A. & Tinbergen L. 1939. De verspreiding der kleine zwanen, *Cygnus b. bewickii* Yarr., in de Zuiderzee, vóór en na de verzoeting. *Limosa* 12: 1–18.
- Dickman C.R. 1992. Commensal and mutualistic interactions among terrestrial vertebrates. *Trends Ecol. Evol.* 7: 194–197.
- Dijksen A.J. & Ouweneel G.L. 2005. Commensalism between Black-necked Grebes *Podiceps nigricollis* and Mute Swans *Cygnus olor*. *Limosa* 78: 155–156.
- Dubois F. & Giraldeau L.-A. 2005. Fighting for resources: the economics of defence and appropriation. *Ecology* 86: 3–11.
- Ens B.J. & Goss-Custard J.D. 1984. Interference among Oystercatchers *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *J. Anim. Ecol.* 53: 217–231.
- Goodale E. & Kotagama S.W. 2008. Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behav. Ecol.* 19: 887–894.
- Gyimesi A., Varghese S., de Leeuw J. & Nolet B.A. 2012. Net energy intake rate as a common currency to explain swan spatial distribution in a shallow lake. *Wetlands* 32: 119–127.
- Hidding B., Nolet B.A., de Boer T., de Vries P.P. & Klaassen M. 2010. Above- and below-ground vertebrate herbivory may each favour a different subordinate species in an aquatic plant community. *Oecologia* 162: 199–208.
- Hino T. 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. *J. Avian Biol.* 29: 17–24.
- Källander H. 2005. Commensal association of waterfowl with feeding swans. *Waterbirds* 28: 326–330.
- Klaassen R.H.G., Nolet B.A. & Bankert D. 2006. Movement of foraging tundra swans explained by spatial pattern in cryptic food densities. *Ecology* 87: 2244–2254.
- Lovvorn J.R. & Gillingham M.P. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77: 435–451.
- Nolet B.A., Bevan R.M., Klaassen M., Langevoord O. & van der Heijden Y. 2002. Habitat switching by Bewick's swans: maximization of average long-term energy gain? *J. Anim. Ecol.* 71: 979–993.
- Nolet B.A., Fuld V.N. & van Rijswijk M.E.C. 2006a. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* 112: 353–362.
- Nolet B.A. & Klaassen M. 2005. Time and energy constraints in demanding phases of the annual cycle: an example of time limitation in refuelling migratory swans. *Oikos* 111: 302–310.
- Nolet B.A., Klaassen R.H.G. & Mooij W.M. 2006b. The use of a flexible patch leaving rule under exploitative competition: a field test with swans. *Oikos* 112: 342–352.
- Nolet B.A., Langevoord O., Bevan R.M., Engelaar K.R., Klaassen M., Mulder R.J.W. & van Dijk S. 2001. Spatial variation in tuber depletion by swans explained by differences in net intake rates. *Ecology* 82: 1655–1667.
- Percival S.M. & Evans P.R. 1997. Brent Geese *Branta bernicla* and *Zostera*; Factors affecting the exploitation of a seasonally declining food resource. *Ibis* 139: 121–128.
- Petrie S.A., Badzinski S.S. & Wilcox K.L. 2002. Population trends and habitat use of Tundra Swans staging at Long Point, Lake Erie. *Waterbirds* 25: 143–149.
- Pot R. 1984. The development of *Potamogeton* vegetation in the Lauwersmeer. *Acta Botanica Neerlandica* 33: 361–362.
- Royama T. 1971. Evolutionary significance of predators' response to local differences in prey density: a theoretical study. In: den Boer P.J. & Gadwell G.R. (eds) Dynamics of populations. PUDOC, Wageningen, pp. 344–357.
- Sherwood G.A. 1960. The Whistling Swan in the West with particular reference to Great Salt Lake Valley, Utah. *Condor* 62: 370–376.

- Sridhar H., Beauchamp G. & Shanker K. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78: 337–347.
- Stienen E.W.M. & Brenninkmeijer A. 1999. Keep the chicks moving: how Sandwich terns can minimize kleptoparasitism by black-headed gulls. *Anim. Behav.* 57: 1135–1144.
- Sutherland W.J. & Allport G.A. 1994. A spatial depletion model of the interaction between Bean Geese and Wigeon with the consequences for habitat management. *J. Anim. Ecol.* 63: 51–59.
- van Eerden M.R., Beekman J.H., Smit M. & Oosterbeek K. 1997. Patch use by Bewick's Swans *Cygnus columbianus bewickii* feeding upon Sago Pondweed *Potamogeton pectinatus* in shallow lakes in the Netherlands: variation in exploitation thresholds caused by social, environmental and time dependent factors. In: van Eerden M.R. (ed.) *Patchwork*. Rijkswaterstaat, Directie IJsselmeergebied, Lelystad, pp. 187–214.
- van Wijk R.J. 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. *Aquatic Botany* 31: 211–258.
- Wanink J.H. & Zwarts L. 2001. Rate-maximizing optimality models predict when Oystercatchers exploit a cohort of the bivalve *Scrobicularia plana* over a 7-year time span. *J. Anim. Ecol.* 70: 150–158.

SAMENVATTING

Aquatisch foeragerende Kleine Zwanen *Cygnus bewickii* worden vaak vergezeld door duikeenden, maar de precieze aard van deze relatie is onbekend. Kleine Zwanen trappelen een kuil om knolletjes van waterplanten op te graven. De duikeenden worden algemeen verondersteld te profiteren, al dan niet door voedsel van de zwanen te stelen (kleptoparasitisme versus commensalisme). Ook onze veldwaarnemingen in het Lauwersmeer toonden een sterke correlatie tussen het aantal foeragerende zwanen en het aantal foeragerende Tafeleenden *Aythya ferina* en Kuifeenden *A. fuligula*, met een mediane verhouding van ongeveer 1 duikeend per zwaan. Om te bepalen of deze associatie kleptoparasitair of commensaal was, hebben we in een serie experimentele metingen de opnamesnelheid gemeten van Kleine Zwanen en Tafeleenden als ze alleen of samen foerageerden. Gemiddeld haalden de Tafeleenden een tweemaal zo hoge opnamesnelheid in gezelschap van een Kleine Zwaan als wanneer ze alleen foerageerden. De Tafeleenden stalen geen voedsel, maar profiteerden van voedsel dat uit de kuil wegdreef na het trappelen van de zwanen. De opnamesnelheid van de Kleine Zwanen was niet lager in de aanwezigheid van een Tafeleend. We concluderen dat de relatie commensaal is, waarbij de duikeenden profiteren zonder negatief effect op de zwanen (althans op de korte termijn).

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