

Modelling state-dependent interference in common cranes

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Summary

1. Interference is a key component of food competition, but is difficult to measure in natural animal populations. Using data from a long-term study, we show that interference between common cranes *Grus grus* L., feeding on patches of cereal seeds, reduces intake rates at high competitor densities, and that the strength of interference is unrelated to food abundance.

2. An alternative to measuring interference directly is to predict its strength using behaviour-based models. We test an interference model, originally developed for shorebirds feeding on invertebrate prey, for cranes. We compare the predictions of a *rate-maximizing* model, in which animals steal food if this increases intake rate, and a *state-dependent* model, in which they only rate-maximize if their intake rate is below a target value, otherwise they minimize injury risk by not stealing food. State-dependent aggression occurs in cranes.

3. The state-dependent model predicts more accurately the relative aggression rates of cranes of different dominance. However, both models predict accurately the observed strength of interference, that the strength of interference is unrelated to food abundance, at least within the observed range of crane and seed densities, and that cranes of a higher dominance have a higher intake rate than those of lower dominance.

4. This paper shows how state-dependent behaviour can be incorporated into an interference model, and that the model can produce accurate predictions for a system quite different to that for which it was developed.

Key-words: dominance, *Grus grus*, kleptoparasitism, injury risk, starvation risk.

Journal of Animal Ecology (2002) **71**, 874–882

Introduction

Interference is one of the major components of food competition, but is difficult to measure in natural animal populations. An alternative is to predict the strength of interference using behaviour-based models (e.g. Ruxton, Gurney & de Roos 1992; Holmgren 1995; Stillman, Caldow & Goss-Custard 1997). Interference occurs in most of these models when animals encounter competitors and either waste foraging time by avoiding

or fighting over food or lose food stolen by competitors. Existing interference models have assumed either that animals respond in a fixed way to encounters (e.g. Ruxton *et al.* 1992; Holmgren 1995) or that they adopt the response which maximizes their intake rate (e.g. Stillman *et al.* 1997; Broom & Ruxton 1998). Although models incorporating rate-maximizing decision rules have provided more accurate predictions than fixed rules for one system (Stillman *et al.* 1997), other rules may be more appropriate for other systems (e.g. Houston & McNamara 1999). An alternative rule is that the response of animals will also depend on the relative risks of injury associated with different responses. This may lead to state-dependent behaviour in which animals minimize their risk of injury when feeding conditions are good, but maximize their intake rate when feeding conditions are poor, even though this may increase their chances of injury.

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State-dependent responses to competitors have been observed in common cranes *Grus grus* L. feeding on cereal seeds (Bautista, Alonso & Alonso 1998). Cranes attacked others feeding at higher rates than average birds in the flock. The immediate consequences of a successful attack were an increase in intake rate for the aggressor and a decrease for the victim. Aggression was state-dependent; the intake rate of the aggressor prior to the attack was, on average, lower than that necessary to meet its requirements. Attacks from cranes foraging at higher rates than their flock mates were scarcely observed. Cranes thus used a kleptoparasitic strategy to recover from temporary reductions in intake rate. Crane behaviour is also compatible with the requirements of a producer–scrounger system (Vickery *et al.* 1991). However, the scrounger strategy must be infrequent in the cereal–crane system, characterized by low aggression rates and small net gains for the aggressors (Bautista *et al.* 1998). Studies of the crane–cereal system show that animals may have state-dependent responses to competitors and indicate that this behaviour may be determined by simple decision rules.

In this paper we investigate whether kleptoparasitic interactions lead to interference in cranes (i.e. a reduction in intake rate with increasing competitor density), and test the predictive power of two new versions of an interference model developed previously for shorebirds Charadrii (Stillman *et al.* 1997). In the *rate-maximizing* model, animals steal food if this increases their intake rate, and in the *state-dependent* model, they only rate-maximize if their intake rate is below a target value, otherwise they minimize injury risk by not stealing food.

The model

FORAGING BEHAVIOUR

The model is described by Stillman *et al.* (1997, 2000). It is individual-based and spatially explicit and follows the foraging decisions of each animal as it encounters food and competitors within a two dimensional patch. Prey are distributed randomly within the patch and are not depleted during simulations. The model progresses in discrete time steps, during each of which each animal is in one of four behavioural states: *searching* for food, *handling* food, *avoiding* competitors or *fighting* with competitors over food. Searching animals move at speed, v , in a straight line and have a constant probability, λ per time step, of capturing food from the patch. After capturing food, animals remain stationary and spend a fixed amount of time, H , consuming it before resuming searching. If a searching animal comes within the encounter distance, D , of any other, it may avoid it by moving directly away, in a straight line, at a constant speed, v , until they are separated by more than the encounter distance. We term this an *avoidance encounter*. While avoiding, animals cannot capture or steal food. If a searching animal comes within the encounter distance, D , of another which is handling

food, it may start a fight to steal the food. We term this a *fight encounter*. The model assumes that, once attacked, handling animals always fight over their food. Fights last for a fixed amount of time, K , and their outcome depends on the relative dominance of the two animals. For simplicity, we assume here that the winner of a fight always retains/steals the food. Stillman *et al.* (1997) assumed that an aggressor did not always steal the food even if it won the fight. We assume a linear dominance hierarchy so that the more dominant animal in a dispute always wins regardless of the absolute difference in dominance between the competitors. The loser of the dispute avoids the winner by moving directly away, in a straight line, at constant speed, v , until separated by more than the encounter distance, D . While avoiding, the loser cannot capture or steal food. For the purpose of modelling the crane–cereal system, the model was altered so that food was consumed continuously throughout handling time (mimicking the depletion of a patch), instead of instantaneously at the end of the handling time.

DECISION RULES

Rate-maximizing decision rules are incorporated using the approach described by Stillman *et al.* (1997, 2000). Each time an animal encounters another, the model compares its expected intake rate if it avoids (avoidance encounters) or fights (fight encounters) with that expected if it ignores the competitor and continues to search. Animals adopt the response that maximizes their expected intake rate, or have a 50% chance of either response if expected intake rates are equal. With rate-maximizing rules, the only cost to aggression is lost feeding time.

State-dependent decision rules are incorporated using the following approach. We assume that stealing food has a higher risk of death through injury during a fight than capturing food independently; the cost of aggression is both lost feeding time and increased injury risk. If an animal's average intake rate from the start of a simulation is below the *target intake rate*, it rate-maximizes in the same way as in the rate-maximizing model. If an animal's average intake rate is greater than the target intake rate it minimizes its risk of injury by not attempting to steal food and always avoiding competitors. We assume that, as fighting is more risky than searching independently, searching for food and avoiding competitors are the default behaviours. This means that at the start of simulations all animals avoid dominant competitors and do not fight, and resort to fighting only if their intake rate is below the target. The model assumes that handling animals always fight over their prey when attacked, and so dominant aggressors are still exposed to the risk of injury when attacking others, even though they always ultimately win the dispute and steal the food. The only differences between the two versions of the model are that the state-dependent model has one additional parameter,

the target intake rate, and animals in this model risk-minimize when their average intake rate exceeds the target intake.

The model assumes that individuals know the dominance of competitors. It is probable that individual cranes can recognize each other's rank by variation in size, plumage and/or behaviour without necessarily being involved in an aggressive encounter.

MODELLING THE CRANE-CEREAL SYSTEM

Cranes forage in large flocks in cereal fields (wheat and barley, Alonso, Alonso & Bautista 1994) around Laguna de Gallocanta, NE Spain (40°58'N, 1°30'W). The system was suitable to test the model because it has been studied intensively over last two decades, and because the simplicity of the habitat structure and the crane's diet allowed parameters to be measured accurately. Alonso *et al.* (1994, 1995) and Bautista, Alonso & Alonso (1992) give full details of the study site and field methods.

During winter, cranes feed on cereal seeds buried 2–3 cm below ground level. Cranes walk slowly across a field making sideward movements with their bill to remove the surface earth to locate individual seeds. Occasionally groups of seeds are discovered, allowing the crane to eat several seeds without walking, although some additional digging may be required. We refer to such a group of seeds as a *patch*, although note that Alonso *et al.* (1995) defined a patch as the cereal field occupied by a flock. Cranes fight over patches of seed rather than individual seeds, which are each consumed very quickly. This meant that encounter rate (λ) and handling time (H) in the model referred to feeding patches rather than to individual seeds, and that birds consumed a fixed amount of seeds (E) while feeding in a patch.

Patch encounter rate (λ), handling time (H) and the number of seeds eaten per patch (E) were measured from a subsample of 92 independent observations periods recorded in a radio-tracking study in the study area between 1989 and 1992. Birds were observed for 60–420 s with $\times 60$ –90 telescopes from distances of 500–1000 m to avoid disturbance, and food intake

measured by counting the number of swallowing movements. A patch was defined when more than five seeds were ingested between two steps. A total of 105 patches in 92 observation periods were identified. Data for patches were averaged over patches when more than one patch was found in the same observation period. The model was parameterized using three combinations of this dataset to determine whether site quality affected crane behaviour. *All sites*: data from all fields, irrespective of their quality. *Rich sites*: data from fields in which the average intake rate of the flock (seeds s^{-1}) was above that required to meet energy requirements (i.e. the starvation threshold intake rate (Alonso *et al.* 1995)). *Poor sites*: data from fields in which the average intake rate of the flock was below the starvation threshold intake rate. For each data set we calculated the average rate at which cranes encountered patches of seed (λ), the average time spent within a patch (H) and the average number of seeds eaten in a patch (E) (Table 1).

Movement speed ($v = 0.099$ (SE = 0.005) ms^{-1}) and the duration of kleptoparasitic disputes ($K = 4$ (SE = 0.1) s) were measured in a previous study of kleptoparasitic behaviour in cranes (Bautista *et al.* 1998). Bautista *et al.* (1998) found no relationship between kleptoparasitic dispute time and the average intake rate of a flock, and so we used the same value of K in rich and poor sites. Encounter distance ($D = 1.59$ (SE = 0.12) m) was taken to be the average of (i) the minimum distance to which foraging cranes normally allow others to approach and (ii) the nearest neighbour distance at which they most frequently change direction. As insufficient data were available for sites of different quality, we assumed that encounter distance was the same in rich and poor sites. The state-dependent model also needed an additional parameter, the target intake rate (T), above which cranes risk-minimize and below which they rate-maximize. The target intake rate was calculated from the starvation threshold intake rate (Alonso *et al.* 1995). Cranes do not obtain all of their intake from within patches, about 19% was obtained from individual seeds consumed while moving between patches in the data used in this study. The model did not incorporate the intake of seeds between patches, as

Table 1. Parameter values (mean \pm standard error) and profitabilities for cereal-feeding cranes. λ , H and E were calculated separately from all, rich and poor sites. v , K and D were only calculated from all sites and their values are given in the text. The profitability of searching was $E/((1/\lambda) + H)$ (Holling 1959) and the profitability of food stealing from a subdominant competitor ($E/2)/(K + (H/2))$ (adapted from Stillman *et al.* (1997) by assuming that attacks occur halfway through handling time and half the initial seeds remain)

	All sites ($n = 92$)	Rich sites ($n = 47$)	Poor sites ($n = 43$)	Units
Patch encounter rate (λ)	0.0115 \pm 0.007	0.0121 \pm 0.008	0.0100 \pm 0.006	patches s^{-1}
Patch handling time (H)	56 \pm 4	53 \pm 6	60 \pm 5	s
Number of seeds eaten in each patch (E)	15.5 \pm 1.0	16.4 \pm 1.6	14.6 \pm 1.1	
Profitability of searching	0.108	0.121	0.091	seeds s^{-1}
Profitability of stealing	0.242	0.269	0.215	seeds s^{-1}

Table 2. Method and parameters used to calculate the target intake rate of cereal-feeding cranes obtained from within patches. The target intake rate excludes the intake rate obtained between patches as this source of intake was not modelled. The standard error of P_{Between} could not be estimated, as only a single value was calculated for this parameter. The standard errors of $I_{\text{FromBetween}}$ and T were calculated from the standard errors of the parameters used their calculations

Parameter	Value	Units	Calculation
Starvation threshold intake rate ($I_{\text{Starvation}}$)*	0.156 (SE = 0.003)	seeds s ⁻¹	
Proportion of time between patches (P_{Between})	0.608		
Intake rate when between patches ($I_{\text{WhenBetween}}$)	0.064 (SE = 0.009)	seeds s ⁻¹	
Intake rate obtained from between patches ($I_{\text{FromBetween}}$)	0.039 (SE = 0.009)	seeds s ⁻¹	= $P_{\text{between}} I_{\text{between}}$
Target intake rate from patches (T)	0.117 (SE = 0.006)	seeds s ⁻¹	= $I_{\text{Starvation}} - I_{\text{WhenBetween}}$

*From Alonso *et al.* (1995).

cranes do not fight over individual seeds, and so the target intake rate was calculated from the starvation threshold intake rate minus the intake rate obtained from between patches (Table 2). The value of T was assumed to be the same in rich and poor patches, as a crane's target intake rate is unlikely to be influenced greatly by site quality.

The observed strength of interference was measured by relating intake rate to competitor density. To determine whether site quality affected the strength of interference, separate relationships were generated from data from all, rich or poor sites. Competitor density was measured from the spacing of birds using the following procedure. The mean interbird distance (I bird lengths) within a flock was estimated as a multiple of body length. The radius (r m) of a circular area occupied by each bird in a flock was calculated from

$$r = b \left(\frac{I + 1}{2} \right), \quad \text{eqn 1}$$

where b = bird length (= 0.8 m). The term in parenthesis calculates (in bird lengths) half the average distance between a focal bird and its neighbours, including the width of the birds themselves. Competitor density (C birds ha⁻¹) was estimated from the inverse of the circular area occupied by each bird

$$C = \frac{10\,000}{\pi r^2}. \quad \text{eqn 2}$$

SIMULATION STRATEGY

Each of the model's parameters were measured empirically and so each had an associated error. To determine the sensitivity of the model's predictions to uncertainty in parameter values, simulations were run with a range of values for each parameter, rather than just the mean value. Predictions for each competitor density were obtained by running 200 simulations. At the start of each simulation, the value of each parameter was drawn from a normal distribution with the appropriate mean and standard error. Results are presented as the 95% confidence interval for predictions, calculated by excluding the 2.5% lowest and 2.5% highest predictions.

Results

OBSERVED STRENGTH OF INTERFERENCE IN CRANES

Patch stealing was profitable for cranes regardless of site quality (Table 1); a crane could increase its intake rate by stealing a patch from a less dominant crane instead of continuing to search independently. This happened because the time to steal a patch was short in comparison with the time to find a patch independently. In contrast, being attacked reduced the intake rate of victims as they wasted time in the dispute and were displaced from their foraging patch (Bautista *et al.* 1998). Furthermore, across all sites, intake rate decreased with increasing competitor density (Fig. 1a; Table 3). It is unlikely that this reduction in intake rate was caused by resource depletion because, during winter, cranes consumed only 5% of buried seed in sown cereal fields (Alonso, Alonso & Veiga 1984; Alonso *et al.* 1994), and cranes showed a marked tendency to forage day after day in the same areas (Alonso, Alonso & Veiga 1987), signalling that depletion was not the main factor determining their distribution. The combination of patch stealing and reduced intake rates at high competitor densities was evidence that interference occurred. Although intake rate was negatively related to competitor density in poor sites but not in rich sites (Fig. 1b; Table 3), a direct comparison of the slopes showed that they were not statistically different ($F_{1,117} = 0.2$, $P = 0.96$; parallelism test in analysis of covariance). We concluded, therefore, that the strength of interference was not related to site quality, at least within the range of seed and crane densities observed.

As the mechanism of interference in cranes is patch stealing by more dominant birds from less dominant birds, at high competitor densities, cranes of lower dominance should have lower intake rates than those of higher dominance. Insufficient data were available to relate intake rate to competitor density for birds of known dominance. However, in a previous study average intake rate, over a range of sites and competitor densities, was related positively to dominance ($r = 0.677$, $n = 12$, $P = 0.02$, Pearson correlation coefficient; Bautista, Alonso & Alonso 1995; Fig. 2a). Low dominance

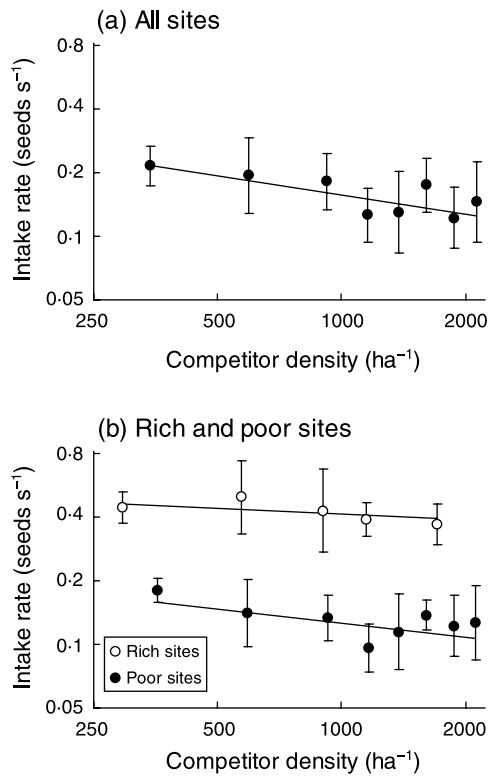


Fig. 1. Observed relationships between intake rate and competitor density in cereal-feeding cranes feeding in sites of differing quality. The symbols show grouped means ($\pm 95\%$ confidence limits). The number of groups differs between rich and poor sites as, due to low sample sizes, some were merged for rich sites. The lines show linear regression relationships of \ln transformed intake rate against \ln transformed competitor density (Table 3).

cranes had intake rates below the flock average, while high dominance cranes had intake rates above the flock average.

The strength of interference in cranes is likely to depend on the aggression rates of individuals of differing dominance. In a previous study, across a range of sites of all qualities and competitor densities, the aggression rates of medium dominance cranes were not significantly different from the flock average, while those of low and high dominance cranes were lower than the flock average (Alonso, Bautista & Alonso 1997; Fig. 2b). However, in a direct comparison between both groups, there was no significant difference between the

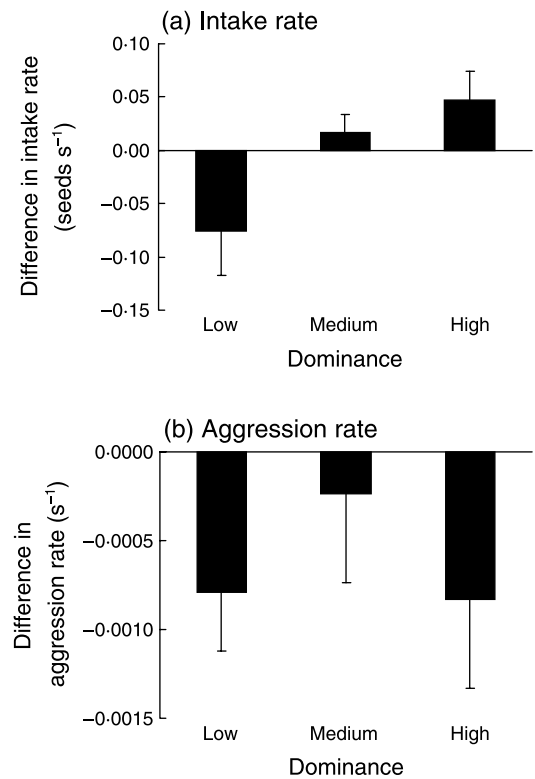


Fig. 2. Observed relationships between dominance and (a) intake rate and (b) aggression rate in cereal-feeding cranes. Different cranes were observed in different sites, and so to standardize for site quality and competitor density, both intake rate and aggression rate are expressed relative to flock averages. The bars show means and associated standard errors of birds within each dominance range: low – $< 33\%$ of encounters won ($n = 4$); medium – $34–66\%$ won ($n = 6$); high – $> 66\%$ won ($n = 3$). (a) Redrawn from Bautista *et al.* (1995) and (b) from Alonso *et al.* (1997). Aggression rate includes both attacks which are initiated and received.

aggression rates of medium dominance cranes and those of high or low dominance ($P = 0.086$, $n_1 = 7$, $n_2 = 6$, Mann–Whitney U -test), and there was no relationship between dominance and aggression rate ($r = -0.0003$, $n = 13$, $P > 0.99$, Pearson correlation coefficient). Insufficient data were available from birds of known dominance for separate analyses in sites of differing quality or to show how aggression rate varied with competitor density. We concluded that aggression rate was not related to dominance.

Table 3. Relationships between intake rate (seeds s^{-1} , \ln transformed) and competitor density (ha^{-1} , \ln transformed) for cereal-feeding common cranes. Regressions were performed on data collected from all, rich or poor sites. The first two rows show the regression coefficients and associated standard errors. The last row shows the intake rate predicted at 400 birds ha^{-1}

	All sites	Rich sites	Poor sites
Intercept	0.211 (± 0.784)	-0.285 (± 0.728)	-0.588 (± 0.716)
Competitor density	-0.301 (± 0.113)	-0.089 (± 0.107)	-0.217 (± 0.103)
n	121	23	98
P	< 0.01	NS	< 0.05
Intake rate at 400 birds ha^{-1}	0.204 seeds s^{-1}	0.441 seeds s^{-1}	0.151 seeds s^{-1}

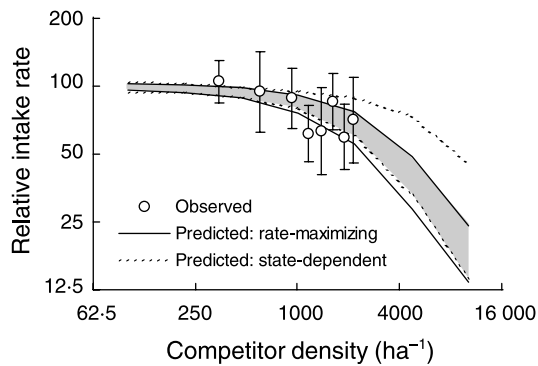


Fig. 3. Predicted and observed relationships between intake rate and competitor density in cereal-feeding cranes. Observations are grouped means ($\pm 95\%$ confidence limits) calculated from data collected from all sites. Predictions are 95% confidence intervals derived from the state-dependent and rate-maximizing models. The shaded area shows the overlap in the predictions of the two models. Both observed and predicted intake rates are plotted as a percentage of intake rate in the absence of interference (Table 3 shows the observed intake rate at 400 birds ha^{-1} , from which the observed relative intake rate was calculated; this density was chosen as it was the lowest density at which cranes were observed).

PREDICTED STRENGTH OF INTERFERENCE IN CRANES

We tested whether the state-dependent and rate-maximizing models accurately predicted (1) the

observed strength of interference (Fig. 1a), (2) that the strength of interference was the same in rich and poor quality sites (Fig. 1b), (3) that intake rate increased with increasing dominance (Fig. 2a) and (4) that aggression rate was unrelated to dominance (Fig. 2b).

Test 1: Strength of interference

Across all sites, both models predicted similar strengths of interference, which were also similar to that observed (Fig. 3). Both models predicted the observed intake rate with similar accuracy across the full range of observed competitor densities; in both models, predictions overlapped the 95% confidence intervals of the observed data in all eight of the competitor density ranges.

Test 2: Site quality and the strength of interference

In poor sites, both models produced very similar predictions, and accurately predicted the observed strength of interference (Fig. 4a); predictions overlapped the 95% confidence intervals of the observed data in seven of the eight competitor density ranges. Predictions differed more in the rich sites, with the state-dependent model predicting a wider range of intake rates (Fig. 4b). However, the 95% confidence intervals of the two models overlapped each other, and both accurately predicted the observed intake rate; predictions overlapped the 95% confidence intervals of the observed data in all five of the competitor density

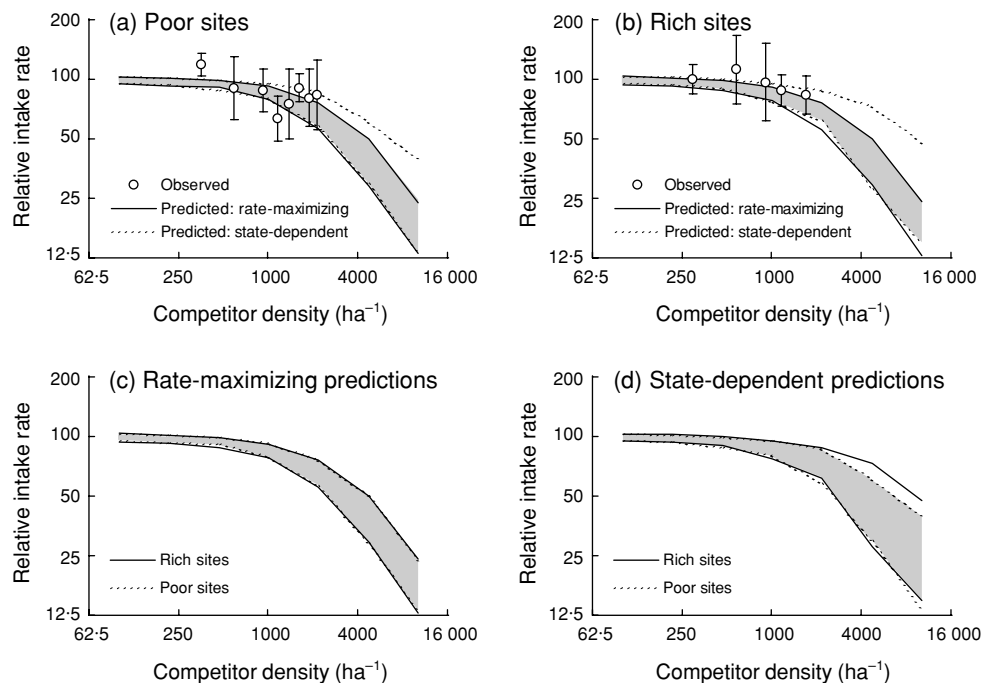


Fig. 4. Effect of site quality on the predicted and observed relationships between intake rate and competitor density in cereal-feeding cranes. Observations are grouped means ($\pm 95\%$ confidence limits) and predictions are 95% confidence intervals derived from the state-dependent and rate-maximizing models. The shaded areas show the overlap in predictions. The observed data and model parameters (Table 1) are calculated from rich or poor sites. Both observed and predicted intake rates are plotted as a percentage of intake rate in the absence of interference (Table 3 shows the observed intake rate at 400 birds ha^{-1} , from which the observed relative intake rate was calculated).

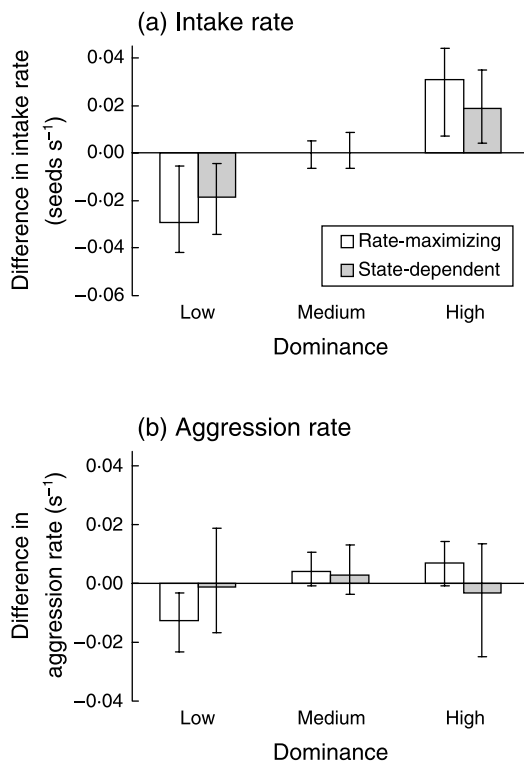


Fig. 5. Predicted relationships between dominance and (a) intake rate and (b) aggression rate in cereal-feeding common cranes at a competitor density of 1000 birds ha⁻¹. The model assumed either rate-maximizing (open bars) or state-dependent (shaded bars) decision rules. Parameters (Table 1) were calculated from all sites. The bars show means and associated 95% confidence intervals for predictions within each dominance range. As replicate simulations were based on different parameter values, predictions for each dominance range are expressed as a difference from the flock average. Aggression rate includes both attacks which are initiated and received.

ranges. The predictions of the rate-maximizing model were not influenced by site quality (Fig. 4c), whereas the state-dependent model predicted a wider range of intake rates in rich sites (Fig. 4d). However, the 95% confidence intervals of the state-dependent model in rich and poor sites overlapped, and so neither model predicted that the strength of interference was related to site quality.

Test 3: Dominance and intake rate

The observed relationship between dominance and intake rate was measured across a range of sites of varying quality, and so was compared with the rate-maximizing and state-dependent predictions for all sites. Both models predicted successfully that intake rate was positively related to dominance (Fig. 5a). In both models, low dominance birds had intake rates below the flock average, while high dominance birds had intake rates above the flock average. Even though intake rate increased with increased dominance in both model predictions and field observations, we cannot confirm whether the same mechanism lead to these

relationships. For example, we cannot confirm whether low intake rate in cranes is caused by low dominance (as in the model), or whether low dominance is caused by low intake rate, although we expect the former to be the case.

The state-dependent model predicted less individual variation in intake rate (Fig. 5a); in comparison with the rate-maximizing model, birds of lower dominance had higher intake rates and birds of higher dominance had lower intake rates. This was because in the state-dependent model, the most dominant animals regulated their intake rates to match the target intake rate; they avoided opportunities to steal food, which reduced the amount of interference suffered by less dominant competitors.

Test 4: Dominance and aggression

The observed aggression rate vs. dominance relationship was measured across all sites, and so was compared with the rate-maximizing and state-dependent predictions for all sites. In contrast to observations, the rate-maximizing model predicted that aggression rate was related positively to dominance (Fig. 5b); low dominance birds had intake rates below the flock average, while those of medium and high dominance birds were nearly always above the flock average. More dominant birds encountered handling competitors of lower dominance more frequently and, as they were rate-maximizing, always took these opportunities to steal food. In contrast, the state-dependent model predicted successfully that aggression rate was unrelated to dominance (Fig. 5b). The most dominant individuals had lower aggression rates than in the rate-maximizing model because they only rarely needed to resort to food stealing to meet their target intake; their intake rates were high because they spent little time avoiding competitors. The least dominant individuals were relatively more aggressive than in the rate-maximizing model because the flock average aggression rate was lower. Insufficient field data were available to test the models predictions of the effect of site quality on the aggression rate vs. dominance relationship.

The state-dependent model also predicted that the overall aggression rate varied between sites of different quality; at a density of 1000 birds ha⁻¹, the overall aggression rate per bird was 0.025 attacks s⁻¹ in rich sites and 0.045 attacks s⁻¹ in poor sites. Aggression rate was lower in rich sites because more individuals were able to achieve the target intake rate without needing to resort to kleptoparasitism. The equivalent values for the rate-maximizing model were 0.063 and 0.064 attacks s⁻¹, and so aggression rate was unrelated to site quality in this model.

Discussion

Although competitive interactions between cranes have been observed previously (e.g. Bautista *et al.* 1998), intake rate has not previously been related to

competitor density. The combination of food stealing and a negative relationship between intake rate and competitor density was evidence that interference occurred between cranes.

Both the rate-maximizing and state-dependent models predicted accurately the observed strength of interference, that the strength of interference was unrelated to site quality within the observed range of crane and seed densities and that intake rate increased with increasing dominance. The state-dependent model also successfully predicted that aggression rate was unrelated to dominance. We therefore conclude that the state-dependent model provided a more accurate description of the underlying behaviour from which interference was predicted but that both models equally well predicted the strength of interference itself.

The difference between the predictions of the two models depended on site quality; predictions were more similar in poor than rich sites. The similar predictions in poor sites arose because virtually all animals in the state-dependent model were rate-maximizing, and so behaviour was the same in both models. In rich sites, the most dominant individuals had intake rates above their target intake rate. In the state-dependent model these individuals risk-minimized and did not steal food, whereas in the rate-maximizing model they continued to rate-maximize by stealing food. This risk-minimizing behaviour affected the overall aggression rate and the amount of between-individual variation in susceptibility to interference. Less individual variation was predicted by the state-dependent model because the risk-minimizing behaviour of the most dominant birds both decreased their own intake rate (as they made fewer attacks) and increased the intake rate of the least dominant birds (as they were attacked less). Unfortunately, no suitable field data were available to make the detailed quantitative tests needed to determine which model predicted more accurately the individual variation in intake rate and aggression, and how this varied between sites of different quality.

In common with the rate-maximizing model, an individual-based model of Hemelrijk (1999) also predicted a positive correlation between dominance rank and attack frequency, in contrast to observations in cranes and the predictions of the state-dependent model. Alonso *et al.* (1997) explained the relationship in cranes as injury-risk minimization: subordinate birds avoided attacks from the rest of the flock and dominant birds were avoided by most birds in the flock. Our state-dependent model provides another explanation, not incompatible with the previous one, that dominant birds do not need to resort to food stealing if their intake rates are high and so have lower aggression rates. The state-dependent model also predicted that aggression rate was greater in poor than in rich foraging sites, a common field observation in cranes (Alonso, Veiga & Alonso 1986) and many other animals (Brockmann & Barnard 1979; Huntingford & Turner 1987). Cranes also show enhanced aggressive behaviour

during midwinter, when food availability is minimal (Alonso *et al.* 1984) and the distance between cranes is shorter (Alonso & Alonso 1987).

Our model assumed that animals fought over patches of food rather than, as assumed in previous versions of the model, individual food items (Stillman *et al.* 1997). Cranes handled each seed quickly, making fights over individual seeds impossible. However, the patchy nature of the food meant that it was possible to fight over food patches. Stillman *et al.* (1997) stated that interference will be absent or weak when handling time is short because stealing individual food items is impossible. The present study shows that this may not be the case if food is clumped. In order to parameterize the model for food patch stealing, patch handling time and patch encounter rate were calculated, rather than the handling time or encounter rate with individual food items. The model also assumed that food was consumed throughout handling time, rather than simply at the end, as assumed previously (Stillman *et al.* 1997, 2000). These were minor changes to the model, suggesting that interference over food patches is similar to interference over individual food items.

The interference model used in this paper was tested previously on shorebirds feeding on invertebrate prey (Stillman *et al.* 1997, 2000, 2002). We have shown that the model can be parameterized and produce accurate predictions for a quite different system.

Acknowledgements

We are very grateful to John Goss-Custard, Richard Caldow and Andy West for many useful comments, and to Andy West for help in running simulations. The comments of John Hutchinson and an anonymous referee substantially improved the manuscript. RAS was funded by the Natural Environment Research Council. LMB was partially funded by Ministerio de Ciencia y Tecnología (MCyT) and research grant PB97-1252 of MCyT. Field work was funded by DGICYT project PB87-0389 of the MCyT.

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Received 22 January 2002; revision received 28 May 2002