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Predicting grazing damage by white-fronted geese under different regimes of agricultural management and the physiological consequences for the geese

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Summary

1. One of the most common human–wildlife conflicts is damage by wildlife to agricultural crops. In order to propose cost-effective measures to address wildlife damage and also to manage pest animals that are of conservation interest, both the effects of wildlife on agricultural crop yield and the effects of mitigation measures on wildlife must be evaluated.
2. In this study, we applied a behaviour-based model to the conflict between agricultural production and white-fronted geese *Anser albifrons* causing damage to wheat crops around Lake Miyajimanuma in northern Japan. The model is spatially explicit, individual- and physiology based, and therefore tracks the day-to-day spatial distribution of geese and the physiological dynamics of fat deposition by each goose throughout the staging period.
3. In our simulations, the establishment of alternative feeding areas (AFAs) for the geese was predicted to be cost-effective for alleviating wheat damage if the number of AFAs and the amount of alternative food supplied was balanced carefully. However, even with the most cost-effective combination, a reduction of up to 23% in heavily damaged areas was the best outcome that could be achieved.
4. Alternatively, locating wheat fields further away from the roost site and also encouraging farmers to leave rice grain remains, the main food resource for the geese, could greatly reduce wheat damage without a detrimental impact on the geese (measured in terms of fat deposition) over a wide range of simulated population sizes.
5. *Synthesis and applications*. The suggested combination of mitigation measures (relocation of wheat fields and inhibition of rice-reducing agricultural practices) should qualify to be tested in practice for alleviating agriculture–geese conflicts in the study area. This study demonstrates that behaviour-based models can be applied successfully to agriculture–wildlife conflicts, allowing us to evaluate the effects of mitigation measures by quantitative predictions. Behaviour-based models can be applied to most cases of agriculture–wildlife conflicts involving adaptive foraging behaviour of animals.

Key-words: agricultural damage, agricultural practices, alternative feeding area, *Anser albifrons*, behaviour-based model, mitigation measures, predictive model

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Introduction

Human–wildlife conflicts occur world-wide and include a variety of problems, such as damage to forests and fishery resources, attacks on domestic animals and humans and transmission of disease (Conover 2002; Thirgood, Woodroffe & Rabinowitz 2005). One of the most common and widespread problems, however, is damage by wildlife to agricultural crops (Conover 2002; Osborn & Hill 2005).

In order to address this issue, it is necessary to evaluate not only the effects of wildlife on agricultural crop yield, but also the effects of mitigation measures on the fitness components of wildlife for the following two reasons. Because a high proportion of threatened and vulnerable species live in an agricultural landscape (Ormerod & Watkinson 2000; Green *et al*. 2005; Hole *et al*. 2005), it is possible that a species causing serious agricultural damage will also be of high conservation interest (e.g. Siex & Struhsaker 1999; O'Connell-Rodwell *et al*. 2000; Tourenq *et al*. 2001). However, some mitigation measures such as provision of alternative food can be of benefit to the pest animals, and therefore this can intensify the damage in the long term by increasing the number of pest animals (Conover 2002). Through evaluation of the effects of mitigation measures on fitness components of wildlife, such as foraging success or reproductive success, we should be able to predict the consequent change in population size in pest animals and modify the management strategy accordingly. However, while there has been a number of studies on the impact of wildlife on agricultural crops, few studies also evaluated the impact of mitigation measures on pest animals (Conover 2002; Woodroffe, Thirgood & Rabinowitz 2005; but see Caldow *et al*. 2004 for shellfishery). To date, most studies of agricultural damages by wildlife have been descriptive, even though there is an increasing awareness in conservation biology that predictions, especially quantitative predictions, are necessary to evaluate the cost-effectiveness of mitigation measures (Pettifor, Norris & Rowcliffe 2000a; Beissinger & Mccullough 2002; Sutherland 2005).

The population of white-fronted geese *Anser albifrons* wintering in Japan reflects well such conflict between food production and wildlife conservation. In Japan, destruction of wetlands has restricted goose habitats and the resulting concentration of geese in the remaining habitats has led to serious conflict with agriculture (Miyabayashi 1994). In particular, around Lake Miyajimanuma (43°20′ N, 143°43′ E) the geese forage mainly on the harvest remains of rice, but start to include wheat leaves in their diets when depletion makes rice grains less profitable overall than wheat leaves (Amano *et al*. 2004), causing considerable reduction in wheat yield (Ushiyama 2003). Lake Miyajimanuma is an important staging site for most white-fronted geese wintering in Japan and is visited by a maximum of 65 000 geese (Amano *et al*. 2004), while the whole East Asian population of this species is estimated as 100 000–150 000 (Wetlands International 2002). The geese stay in this area for approximately a month in autumn and again in spring to build up and deposit body fat for migration and reproduction (Moriguchi 2006). Because the number of white-fronted geese has declined dramatically in some Asian countries such as China (Zhang & Lu 1999), both the alleviation of the wheat damage problem and the conservation of goose population staging at Lake Miyajimanuma are important for the conservation of the Asian population of white-fronted geese. In this area, as the depletion of rice grains in late spring drives the geese to forage on wheat (Amano *et al*. 2004), alternative feeding areas (AFAs) are established by distributing waste rice grain to alleviate wheat damage during the spring staging period (Ushiyama 2003). In addition, agricultural practices such as ploughing and collecting straws left in rice fields after harvest and crop diversion, whereby rice fields are turned into alternative crops, are thought to affect not only the foraging success of geese but also the degree of wheat damage by reducing available rice grains (Amano *et al*. 2006b). However, there have been no attempts to quantify the effects of such practices.

In recent years, behaviour-based models have allowed conservation biologists to predict the responses of animal populations to environmental changes (Pettifor, Norris & Rowcliffe 2000a; Sutherland & Norris 2002). Behaviour-based models assume that individuals will behave in a way that maximizes their own fitness (Goss-Custard & Sutherland 1997), allowing robust predictions under novel conditions because, even if conditions change, the basis of predictions, i.e. fitness maximization, will not (Stillman *et al*. 2000; Sutherland & Norris 2002). Although few studies of agricultural damage by wildlife have ever investigated the behavioural processes involved (Tourenq *et al*. 2001; Amano *et al*. 2004), behaviour-based models could become a powerful tool to predict the response of pest animals to mitigation measures because most agricultural damage can be explained by the adaptive foraging behaviour of animals (Messmer 2000; Conover 2002; Amano *et al*. 2004).

The present study applied a behaviour-based model to the conflict between agriculture and white-fronted geese around Lake Miyajimanuma. Intensive empirical studies focusing on the foraging behaviour of geese in this area so far have provided a thorough understanding of the cause of wheat damage (Amano *et al*. 2004). This information can be used in developing a behaviour-based model that predicts spatial distribution and foraging success of geese in the field (Amano *et al*. 2006b). Using this model, we attempted to evaluate the impact of several mitigation measures on the behaviour of white-fronted geese and their consequent foraging success as well as the degree of wheat damage. Expanding on the results, we identified the most effective combination of mitigation measures that could alleviate wheat damage without affecting body fat deposition by geese. In order to explore the long-term impact of the mitigation measures, effectiveness was evaluated under different population size scenarios.

THE MODEL

In an earlier study, we reported that a model assuming incompletely informed foragers with benefits of group foraging (IIFG model) could predict successfully the seasonal changes in spatial distribution, flock size, diets and fat mass accumulated by geese in the field (Amano *et al.* 2006b). In the present study we used this same model to evaluate the impact of mitigation measures. Although the model structure and parameter values are described in detail elsewhere (Amano *et al.* 2006b), the basic structure of the model is described below.

The model is spatially explicit, individual- and physiology based, and therefore tracks the day-to-day spatial distribution of individuals and the dynamics of fat deposition by each individual throughout their staging periods (autumn: 21 September–31 October; spring: 1 April–6 May). A model world was created with two types of discrete foraging patches (rice and wheat). Using the location of actual fields, the model world reproduced all foraging patches (rice: 669; wheat: 544) within 10 km of the roost at Lake Miyajimanuma. A model population of birds (maximum of 36 544 individuals based on field count data in the 2003–04 season) was also created, comprising a number of discrete individuals each with its own unique set of characteristics that influence its foraging success. In the 2003–04 season most of the geese arrived at the study site in three groups (the first around 26 September, the second around 1 October and the third around 9 October) in autumn and in two groups (around 6 April and 23 April) in spring. Based on these field data, during the staging periods in autumn and in spring, an empirically derived number of birds arrive at the model world every day with certain levels of initial fat. During the autumn staging period, rice harvesting is still in progress so birds cannot forage in unharvested rice patches whereas, in early spring, snow cover prevents birds from using some patches. In some rice patches, rice-reducing agricultural practices such as ploughing or collecting straw are carried out. At the beginning of each day, available areas (harvested areas in autumn and snow-free areas in spring), ploughed areas and areas from which straw has been collected in each patch are determined based on field data. For example, we assumed that snow melts earlier in patches further from the roost (mean proportion of snow-free area in wheat patches by 15 April: 77% within 3000 m, 94% between 3000 m and 6000 m, 96% beyond 6000 m from the roost).

At every time step (= 10 min) within the daily active period, each bird decides where to forage across fields with different resource densities by comparing expected gain rates of foraging on rice solitarily, foraging on rice in a flock and foraging on wheat. In this model, we assumed that birds always prefer to join flocks when foraging on wheat because in the field study the sizes of flocks in wheat patches seem to be determined mainly by the relatively small sizes of wheat patches rather than by the trade-off between the costs and benefits of flocking under resource depletion (Amano *et al.* 2006b). Further, resource depletion in wheat patches is unlikely to cause exploitative competition, a cost of flocking, at most resource densities due to the steep increase in the functional response of wheat. Therefore, to make the model as simple as possible, we assumed only one foraging option for wheat (foraging on wheat in a flock). Expected gain rates are updated with individual experience, weighted by the memory factor. In an occupied patch, birds remove food at empirically derived intake rates. The density of rice grains is also reduced by agricultural practices while wheat biomass increases every day due to its own growth. Birds acquire energy through foraging while they also expend energy at different rates, depending on their behaviour. The balance between rates of energy acquisition and expenditure determines each bird's energy reserves. Individuals die when their energy reserves fall to a starvation level. The timing of migration by each bird (i.e. emigration from the model world) is determined by different rules in autumn and in spring.

Model simulations

BASELINE RUNS

The aim of the first model run was to approximate the current level of fat deposition and wheat damage by geese. For input data, we used the field data from the (2003–04) season (Amano *et al.* 2006b).

EFFECTS OF MITIGATION MEASURES

Because the geese start to include wheat leaves in their diets when depletion causes rice grains to be less profitable overall than wheat leaves (Amano *et al.* 2004, 2006b), two types of mitigation measures have the potential to alleviate the wheat damage: (1) increasing the availability of rice and (2) preventing the use of wheat fields. We simulated the effects of these two types of mitigation measures.

The first potential mitigation measure was the provision of alternative feeding areas (AFAs) in spring. Creating AFAs is considered to be one of the effective mitigation measures against grazing damage by the geese and has actually been put into practice in the study area (Ushiyama 2003). We simulated the creation of an AFA by adding 600 kg rice grains in a rice patch on 20 April, following the conventional procedure actually used at the study site. This amount was defined as the 'actual' amount, relative to which some comparisons were made. As AFAs were not established in 2004, following the size and location of AFAs in 2003 six rice patches larger than 2·5 ha were selected randomly for AFA sites, four within 2000 m and two between 2000 m and 3000 m from the roost. Again, this number of AFAs was defined to be 'actual' for comparison purposes. The total area of AFAs created is comparable to approximately 0·4% of the total area of rice fields in the habitat. The effectiveness of AFAs was then simulated with the amount of added rice grains halved and doubled, and with the number of AFAs themselves also halved, doubled and tripled. We then assessed the cost-effectiveness of AFAs with different amounts of food and numbers of AFAs. When calculating the cost of establishing AFAs, we assumed ¥112 kg^{-1} for scattered rice grains and ¥72 975 AFA^{-1} for labour (Department of Agricultural Policy of Bibai city, unpublished data). Damage saved by AFAs (savings) were calculated as follows:

$$Savings = (da_b - da_a) \times ay \times (yl/100) \times ai \qquad \text{eqn 1}$$

where da_b and da_a are the mean area of heavily grazed wheat field (see Output measures) predicted in baseline runs and in runs with AFAs, respectively; *ay* is the average yield of wheat in 2004 (3700 kg ha^{-1}, Department of Agricultural Policy of Bibai city, unpublished data), *yl* is the estimated yield loss caused by goose grazing (25·7%, Ushiyama 2003) and *ai* is the average income from wheat yield in 2004 (¥145 kg^{-1}, Department of Agricultural Policy of Bibai City, unpublished data) in the study site, respectively.

The second mitigation measure simulated for increasing rice availability was inhibiting ploughing and collecting straw from the rice fields; both agricultural practices reduce the amount of rice grains available to the geese by 95·2% and 86·0%, respectively (Amano *et al*. 2006b). Encouraging farmers to leave rice grain remains has been considered as an effective measure for conservation management of the geese in the study area. We also simulated the effects of varying distances of those fields where rice-reducing practices were inhibited from the roost. We compared the results when rice-reducing practices were inhibited in patches within approximately one-third (3000 m) and two-thirds (6000 m) of the total distance from the roost in the model.

The mitigation measure simulated for preventing geese from using wheat fields involved changing the location of the wheat fields. Following examples of refuge creation for geese in Europe (e.g. Vickery & Gill 1999), concentration of rice fields near the roost as refuges for geese together with locating vulnerable wheat fields far from the roost were simulated. These changes in the location of wheat fields were simulated by turning all wheat patches within 3000 m and 6000 m from the roost into rice patches while, at locations beyond 3000 m and 6000 m from the roost, turning rice patches into wheat patches with the same areas as those rice patches transformed from wheat patches.

INTERACTION BETWEEN MITIGATION MEASURES AND POPULATION SIZE

Because depletion of rice grains by geese causes wheat damage in the study site, the degree of wheat damage appears to be related closely to the population size of staging geese. It could be instructive for future policymaking to explore the impact of mitigation measures on fat deposition and wheat damage by geese under different scenarios of population size. Therefore, we first determined the most effective combination of mitigation measures based on the results of simulation runs described above and then simulated the effects of this combination for different goose population sizes by increasing and decreasing the daily number of arrivals by 10%, 25%, 50% and 75%.

OUTPUT MEASURES

We ran 25 simulations arbitrarily with each combination of assumptions and parameter values, and presented the mean predictions with associated 95% confidence limits. None of the predictions under different scenarios for the wide range of parameter values simulated the starvation of an individual during the staging period, which seemed to correspond to field observations, and thus mortality of geese was not used as a fitness component. Instead, foraging success of geese was used to evaluate the impact of mitigation measures on geese. Following Durell *et al*. (2005), foraging success of geese was expressed as the proportion of individuals failing to achieve at least 90% of their target weight (= lower confidence limit of mean target weight) on the migration threshold date, after which geese can migrate once the target weight is reached (Amano *et al*. 2006b). As fat deposition by geese in staging sites has been shown to reflect subsequent survival and breeding success in many goose species (e.g. Ebbinge 1992; Bromley & Jarvis 1993; Ebbinge & Spaans 1995; Schmutz & Ely 1999; Alisauskas 2002; Prop, Black & Shimmings 2003), it seems plausible to use the proportion of geese failing to accumulate their target mass as a fitness component at a staging site. Although the number of white-fronted geese staging in the study site has increased since the 1980s, it has levelled off and appears to have been stable over the last 5 years (T. Amano unpublished data). Hence, the empirically derived body mass at departure in spring 2004 was used as the goose target weight with which the population in the study site would be stable. It should also be noted that fat deposition in a particular staging site might reflect only short-term fitness components, and thus year-round dynamics of the populations need to be considered when assessing long-term fitness of migratory birds (Pettifor *et al*. 2000b; Klaassen *et al*. 2006). It is also true, however, that the study area, Lake Miyajimanuma, is probably one of the most important staging sites for white-fronted geese in Japan in the sense that it is the final staging site for most geese wintering in Japan before the long, over-sea migration to breeding sites (Takekawa *et al*. 2000). Therefore, it seems plausible to assume that fat deposition in this area also has some impact on the long-term fitness of the geese.

On the other hand, the degree of wheat damage was expressed in two ways. First, the cumulative number of geese foraging in wheat fields was calculated as the sum of the daily number of geese predicted to forage in wheat patches. Secondly, the area of heavily damaged wheat fields was calculated as the total area of wheat patches that were exploited by geese after 15 April to half of the mean wheat biomass in late spring (34 g dry wt m^{-2}, T. Amano unpublished data), because heavy grazing by geese in late spring was shown to cause a significant reduction in wheat yield (Ushiyama 2003).

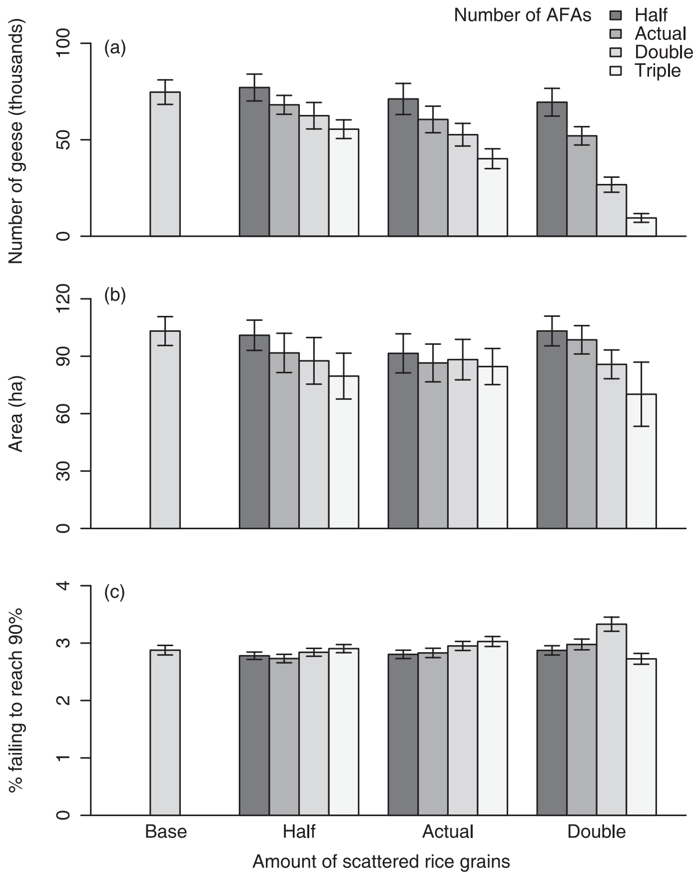

Fig. 1. The predicted effects of establishing alternative feeding areas (AFAs) in different numbers and with various amounts of scattered rice grains on (a) cumulative number of geese foraging on wheat; (b) total area of heavily damaged wheat fields; and (c) proportion of geese failing to reach 90% of their target mass. The number of AFAs and amount of scattered rice grains are shown by defining the values for AFAs actually established in 2003 as 'actual' values. For comparison, the predictions in baseline runs, which approximate the current level of fat deposition and wheat damage by geese, are also shown. Bars represent means and 95% confidence limits.

Results

PREDICTED EFFECTS OF MITIGATION MEASURES

When AFAs were established in the model, the cumulative number of geese foraging on wheat decreased as the number of AFAs and the amount of scattered rice grains per AFA increased (Fig. 1a, Table 1). A significant interaction term indicated that the number of geese foraging on wheat was particularly small when a large number of AFAs with large amounts of rice grains were established. The decrease in the total area of heavily damaged wheat fields due to the presence of AFAs was explained more by an increase in the number of AFAs than the amount of rice grains, which explained only little variance in the area of damaged fields (Fig. 1b, Table 1). Although more geese tended to fail to accumulate 90% of their target reserve as the amount of scattered grains per AFA and the number of AFAs increased, the proportion of geese failing to reach their target weight decreased when the amount of rice grains doubled and the number of AFAs established was tripled (Fig. 1c, Table 1). Although the greatest reduction in wheat damage could be achieved when the amount of rice grains per AFA was doubled and the number of AFAs was tripled, this combination did not lead to high net savings (savings from damage avoidance minus the costs of implementing AFAs) due to high costs of implementation (Fig. 2). Predicted net savings from the implementation of AFAs was highest when the amount of rice grains per AFA was halved and the number of AFAs was tripled (Fig. 2); this had almost no impact on fat deposition by geese (Fig. 1c). Predicted net savings were also high when the 'actual' amount of rice grains was combined with the 'actual' number of AFAs (Fig. 2).

Inhibiting ploughing and collection of straw from rice fields resulted in a decrease in the level of wheat damage, both in the cumulative number of geese foraging on wheat (Fig. 3a) and in areas of heavily damaged wheat fields (Fig. 3b). On the other hand, the proportion of geese failing to accumulate 90% of their target reserves showed little change when those practices were inhibited partially, i.e. only in fields within 3000 m and 6000 m from the roost, although it increased when the inhibition was carried out in all the fields (Fig. 3c).

When wheat fields within 3000 m and 6000 m from the roost were turned into rice fields without changing the total area of wheat fields in the habitat overall, the

Table 1. Results of two-way ANOVA of the effect of rice amount per patch and number of alternative feeding areas (AFAs) established in the model on the degree of wheat damage and fat deposition by white-fronted geese

Response variable	Contributing effects	d.f.	F	P	r^2
Cumulative number of geese foraging on wheat					
	Amount	2,288	79·92	< 0·001	0·21
	Number	3,288	88·48	< 0·001	0·34
	Amount × number	6,288	9·70	< 0·001	0·08
Area of heavily damaged wheat fields					
	Amount	2,288	0·20	0·82	0·001
	Number	3,288	7·83	< 0·001	0·07
	Amount × number	6,288	1·46	0·19	0·03
Proportion of geese failing to accumulate 90% of their target reserves					
	Amount	2,288	14·49	< 0·001	0·06
	Number	3,288	16·03	< 0·001	0·11
	Amount × number	6,288	14·57	< 0·001	0·19

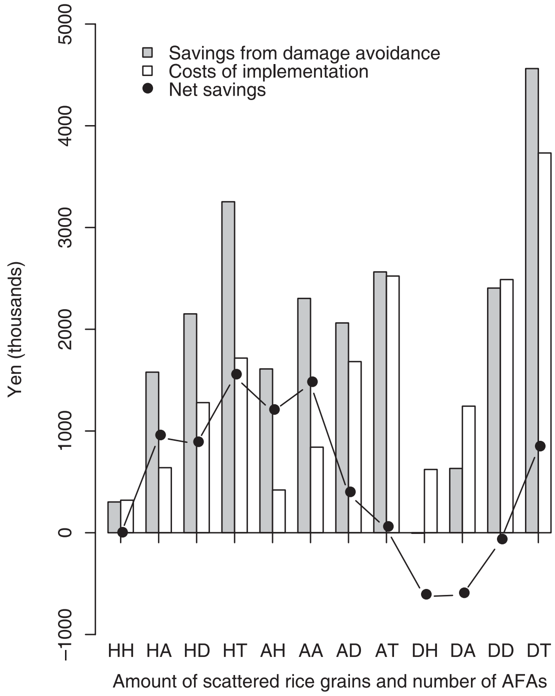

Fig. 2. The estimated cost-effectiveness of alternative feeding areas (AFAs) in different numbers and with various amounts of scattered rice grains. Net savings were calculated by subtracting the costs of implementing AFAs from savings from damage avoidance. Labels on the *x*-axis show the amount of scattered rice grains (left characters) and the number of AFAs (right characters), where values for AFAs actually established in 2003 were defined as 'actual' values and H, A, D and T represent 'half', 'actual', 'double' and 'triple' values, respectively.

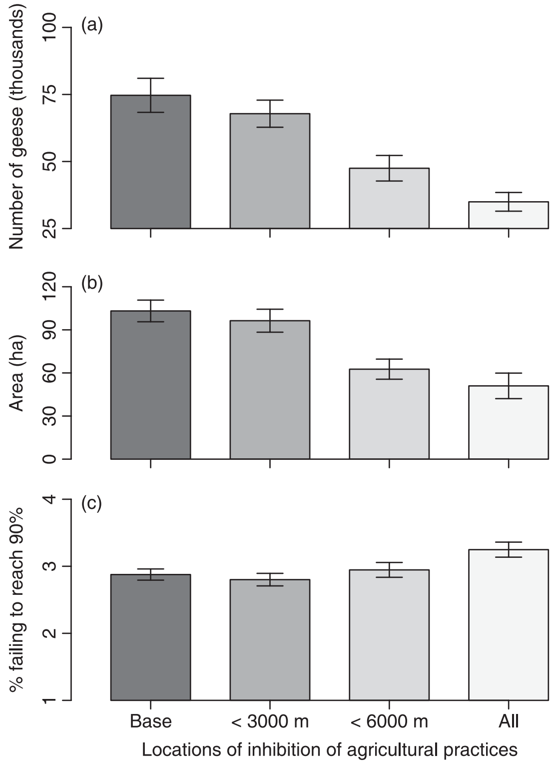

Fig. 3. The predicted effects of inhibiting ploughing and straw-collecting in rice fields on (a) cumulative number of geese foraging on wheat; (b) total area of heavily damaged wheat fields; and (c) proportion of geese failing to reach 90% of their target mass. Labels on the *x*-axis indicate the range of locations of rice fields where ploughing and collection of straw was inhibited; < 3000 m and < 6000 m represent rice fields within 3000 m and 6000 m from the roost, respectively. For comparison, the predictions in baseline runs are also shown. Bars represent means and 95% confidence limits.

area of heavily damaged wheat fields was greatly reduced (Fig. 4b) although the cumulative number of geese foraging on wheat showed only a small change (Fig. 4a). Furthermore, little difference existed between the predicted proportion of geese failing to reach 90% of their target mass in the baseline simulation and in each of the simulations with relocation of wheat fields within 3000 m and 6000 m of the roost (Fig. 4c).

PREDICTED INTERACTION BETWEEN MITIGATION MEASURES AND POPULATION SIZE

Based on the results described above, inhibiting ploughing and collection of straw in rice fields within 6000 m from the roost (one of the two mitigation measures that increase rice availability) was predicted to reduce wheat damage more effectively than creating AFAs without affecting goose fat deposition. It was also revealed that locating wheat fields further from the roost was another effective measure. Therefore, we identified the effective combination of two mitigation measures for alleviating agriculture–goose conflicts as follows: (1) all wheat patches within 6000 m from the roost should be turned into rice patches while, at locations beyond 6000 m from the roost, wheat patches with the same areas as those rice patches transformed from wheat patches are to be created by turning rice patches into wheat patches, and (2) ploughing and collection of straw should be prohibited in the rice fields within 6000 m from the roost.

At the 'actual' population size, the combination of mitigation measures above could greatly reduce wheat damage (96% decrease in the area of heavily damaged wheat fields) with a small impact on the body conditions of geese (Fig. 5). Moreover, wheat damage could be reduced through those mitigation measures under a wide range of goose population sizes while, without those measures, the damage becomes more serious with increasing population size. In particular, these measures managed to keep the area of heavily damaged wheat fields low, except when the population size was increased by 75%, although even with these measures the number of geese foraging on wheat still increased with increasing population size (Fig. 5a,b).

In the absence of effective mitigation measures (above), the proportion of geese failing to reach 90% of their target mass increased when the population size was decreased by 25% and 50%, and decreased again when the population size was decreased by 75% (Fig. 5c). The mitigation measures suppressed this increase in the proportion of geese failing to deposit sufficient fat at low population sizes (Fig. 5c). On the other hand,

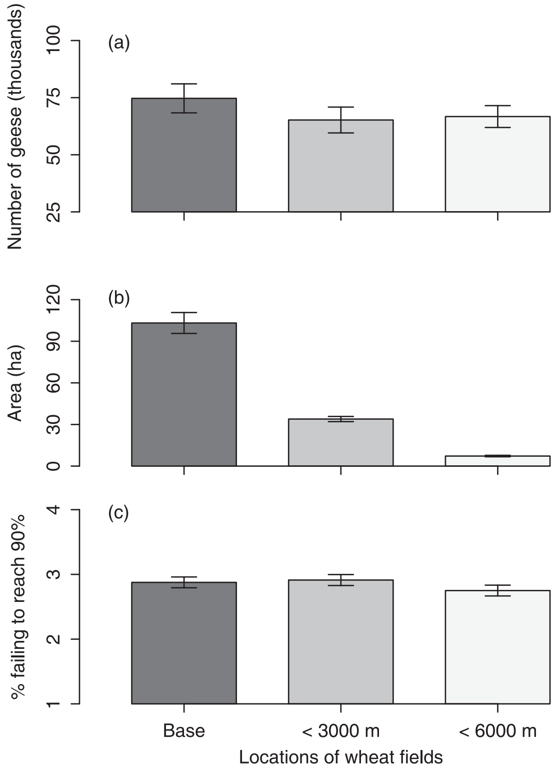

Fig. 4. The predicted effects of replacing wheat fields near the roost with rice fields on (a) cumulative number of geese foraging on wheat; (b) total area of heavily damaged wheat fields; and (c) proportion of geese failing to reach 90% of their target mass. Labels on the *x*-axis indicate the range of locations of diverted wheat fields; < 3000 m and < 6000 m represent the wheat fields within 3000 m and 6000 m from the roost, respectively. For comparison, the predictions in baseline runs are also shown. Bars represent means and 95% confidence limits.

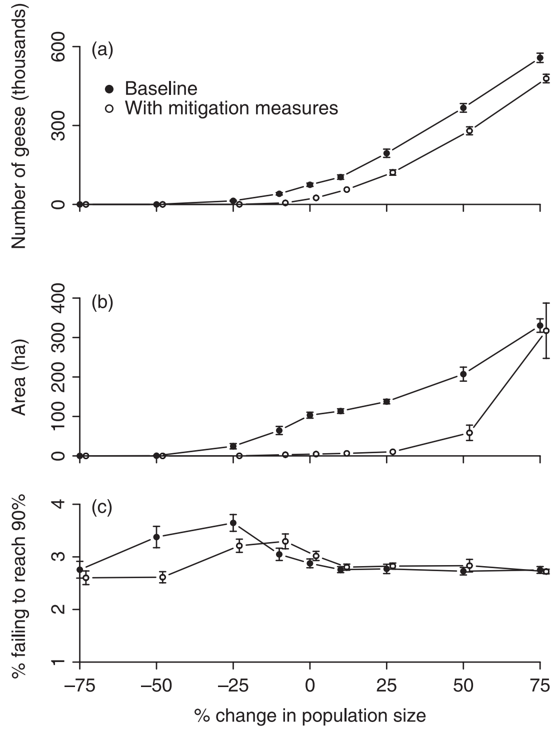

Fig. 5. The predicted interaction between the effective combination of mitigation measures and population size. The effective combination of mitigation measures was simulated by turning all wheat patches within 6000 m from the roost into rice patches while, at locations beyond 6000 m from the roost, creating wheat patches with the same areas as those transformed by turning rice patches into wheat patches, and by ploughing and collection of straw being inhibited in the rice fields within 6000 m from the roost. Predictions are (a) cumulative number of geese foraging on wheat; (b) total area of heavily damaged wheat fields; and (c) proportion of geese failing to reach 90% of their target mass. Bars represent means and 95% confidence limits.

when the population size was increased from the current level, the proportion of geese failing to reach 90% of their target mass did not show any change either with or without the mitigation measures (Fig. 5c).

Discussion

PREDICTED EFFECTS OF MITIGATION MEASURES

In our simulations, alternative feeding areas (AFAs) were predicted to be cost-effective for alleviating wheat damage by geese if their numbers and the amount of rice grains scattered in each were chosen appropriately. The amount of scattered rice grains per AFA had little effect on the area of heavily damaged wheat fields. This result emphasizes the importance of considering incompletely informed foraging by the geese when predicting wheat damage. Because the geese have incomplete information about resource distribution (Amano *et al.* 2006a), having a small number of AFAs with high rice densities would be less effective as AFAs will be detected by only a limited number of individuals, resulting in a small decline in the daily number of geese causing wheat damage from mid-spring onwards. On the other hand, a large number of AFAs with low rice densities would be detected by a large number of geese, but their expected gain rate of rice would increase only slightly. This could delay the timing of a diet shift from rice to wheat in a large number of geese, thereby preventing heavy damage. In mid-spring, wheat biomass is relatively low while the number of staging geese is still large, resulting in a higher level of exploitation of wheat than in late spring. Based on these predictions, we suggest that under a limited budget the number of AFAs should be increased instead of the amount of grains per AFA. Further, our cost-effectiveness analysis showed that increasing costs for AFAs does not lead necessarily to an effective decline in wheat damage. Therefore, we conclude that a threefold number (18) of AFAs with half the amount of scattered rice grains (300 kg) per AFA is the best option although, even with this combination, only up to 23% reduction in damaged areas could be achieved. These predictions would be substantiated further by field experiments in which the amount of grains per AFA and the number of AFAs are varied systematically and the responses of birds are monitored.

When ploughing and collection of straw were inhibited in (1) all rice fields and (2) only the rice fields within 6000 m from the roost, the area of damaged wheat fields was reduced by 51% and 40%, respectively. This suggests that inhibition of rice-reducing agricultural practices prevents geese from shifting their diet to wheat by increasing the expected gain rate of rice. Given the greater reduction in wheat damage with a small impact on fat deposition by geese, inhibition of rice-reducing practices is potentially a more effective mitigation measure than creating AFAs. Not all farmers in the study site plough and collect straw in their fields during the staging periods of geese, but some farmers believe that ploughing and straw-collecting increase soil fertility by accelerating decomposition of remaining straw. In future studies, therefore, investigating whether agricultural practices of this kind increase soil fertility will allow us to evaluate the cost-effectiveness of these measures. On the other hand, inhibition of ploughing and collection of straw in all the fields increased the proportion of geese failing to reach their target mass. This can be explained by the incompletely informed nature of foraging by geese; the increase in overall rice density may delay the diet shift from rice grains, resulting in a great disparity in foraging success.

The area of heavily damaged wheat fields could be greatly reduced by locating wheat fields further from the roost without changing the total area, although this measure did not cause a great reduction in the number of geese foraging on wheat. This result is likely to be because of the difference in biomass among wheat fields along a gradient of distances from the roost. As wheat leaves begin growing after thaw in each field, wheat biomass in spring is higher in fields further from the roost, where snow melts earlier. Therefore, locating wheat fields further from the roost increases wheat biomass, preventing those fields from being exploited to a low biomass (i.e. half of the mean wheat biomass in late spring), even if geese exploit them. Moreover, concentrating rice fields near the roost can prevent them from being missed by the geese altogether, thereby causing a decrease in the number of geese foraging on wheat. This mitigation measure was predicted to have a small impact on goose body conditions and thus seems to be favourable both to farmers and geese. Further research is needed to investigate whether wheat biomass is greater before and even after grazing by geese in fields further from the roost.

PREDICTED INTERACTION BETWEEN MITIGATION MEASURES AND POPULATION SIZE

The combination of relocation of wheat fields and inhibition of ploughing and collection of straw could alleviate successfully wheat damage by geese over a wide range of population sizes. It is noteworthy that the proportion of geese failing to reach their target mass increased when the population size was reduced by 25% and 50% without any mitigation measures. As the decrease in population size delays rice depletion, this result suggests that an improvement in rice patch quality prevents fat deposition by geese. Similar results were obtained when AFAs were established (Fig. 1c) and when rice-reducing practices were inhibited in all the fields (Fig. 3c). These seemingly contradictory results could be explained by the profound disparity in foraging success among geese when foraging on rice due to their incomplete information on patch quality (Amano *et al.* 2006b). As shown in Fig. 5a, when the population size is reduced, the geese become almost entirely dependent on rice grains for food resource, leading to a greater disparity in foraging success of individuals compared to when foraging on wheat leaves with relatively constant profitability. This, in turn, increases the proportion of geese failing to reach their target mass without necessarily decreasing the mean fat mass of the population. This explanation is supported by the following three results. First, when the population size was reduced, the mean fat mass of the population was similar to, and in fact slightly larger than, that at the 'actual' population size (mean fat mass achieved ± 1 standard deviation (s.d.): current population size, 790·1 ± 2·8 g, population size decreased by 25%: 796 ± 2·4 g), which indicated that the decline in population size did not cause an overall decline in fat deposits of the population. Secondly, when the population size was reduced further by 75%, the proportion of geese failing to deposit fat decreased again, which suggests that further relative increase in rice availability offset the effect of uncertainty about rice patch quality by increasing the overall intake rate. Finally, and more importantly, the mitigation measures suppressed the increase in the proportion of geese failing to deposit fat at low population sizes. By locating rice fields close to the roost and inhibiting rice-reducing practices, the mitigation measures seem to reduce the uncertainty regarding rice patch quality, causing a smaller variation in foraging success of individuals. Those mitigation measures are likely, therefore, to prevent further decline in population size at low population sizes. Neither did they seem to cause further increase in population size at high population sizes, because they did not improve fat deposition when the population was increased. In future, to confirm the long-term impact of these predictions, it is essential to keep monitoring the wheat damage and fat deposition by geese after these measures are put into practice.

Conclusions

It should be noted that the model predictions in the present study still remain to be tested experimentally. However, given the good performance of our model in producing patterns of wheat damage and fat deposition by geese observed in the field (Amano *et al.* 2006b), and the advantage of behaviour-based models which allow robust predictions under novel conditions, the suggested combination of mitigation measures (relocation of wheat fields and inhibition of ploughing and collection of straw at patches within 6000 m from the roost) should qualify to be tested in practice by local policy-makers to alleviate agriculture–geese conflicts over a wide range of population sizes. Because the present model could not explore fully the long-term effects on goose population dynamics, it is essential to keep monitoring the effects of the measures discussed in subsequent years. At the same time, detailed information about the target species is often insufficient in the field in conservation management problems. In the present study, despite our lack of knowledge about population parameters of geese in Japan, simulating the effects of mitigation measures under different population sizes made it possible to estimate, at least partially, the long-term effect on the goose population. This approach should be of great help in other systems when applying a relatively complex, information-demanding behaviour-based model.

This study has demonstrated that behaviour-based models can be applied successfully to agriculture–wildlife conflicts, allowing us to evaluate the effects of large-scale mitigation measures both on agricultural damage and on wildlife by quantitative predictions. The effectiveness of behaviour-based models offers promise for many agriculture–wildlife conflicts because most agricultural damage can be explained by adaptive foraging behaviour of animals (Messmer 2000; Conover 2002).

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