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Food supplementation as a conservation intervention: A framework and a case of helping threatened shorebirds at a refuelling site

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ABSTRACT

Supplemental feeding to mitigate the effects of food shortages may in some cases provide critical help to species conservation. However, supplemental feeding may have both positive and negative effects on wildlife and the environment. A scientifically designed feeding project helps to achieve conservation targets and reduces adverse effects. Here, we summarize a three-step framework for food supplementation that we used in practice: (1) determining whether supplemental feeding is required; (2) designing and implementing a practical feeding scheme; and (3) evaluating the effectiveness of food supplementation. We supplemented food for great knots (*Calidris tenuirostris*), an endangered migratory shorebird, at a recently impoverished refuelling site (Yalu Jiang estuary) in the Yellow Sea in spring 2018. The abundance of the staple food of great knots (*Potamocorbula laevis*, which had become very rare after 2012), was insufficient for the birds to refuel before the migratory flight to the breeding grounds. In our practical test, living *P. laevis* were collected in subtidal areas and transported to the intertidal area where great knots had been foraging in earlier years. The supplemented areas attracted 48% of all the great knots present in the 200 km^2 study area. Nearly 90% of the supplemented food was consumed. Most great knots (>80%) foraged in the high-density supplementation zone where the densities of *P. laevis* were restored to the naturally occurring levels in 2011–2012. Here, food intake rates (mg AFDM/s) were 4.2 times those in the adjacent control zones. The framework and the feeding practice should help guide future supplemental feeding in a wide range of species.

1. Introduction

Obtaining sufficient food is the basis for both survival and reproduction. Populations generally tend to grow to ‘carrying capacity’, a level at which no buffering against food declines remains (Newton, 1998). When faced with environmental variations, extreme weather events or human disturbance, food shortages decrease survival and breeding success eventually leading to population declines (Baker et al., 2004; Rakhimberdiev et al., 2015, 2018; Laufenberg et al., 2018). Species with small populations and long life spans (so slow recruitment) have difficulty in recovering once the population declines have set in (Piersma and Baker, 2000). Food supplementation can reduce the risk of population extinction during periods of food shortage (Tian et al., 2019). In the wild, the effects of temporarily reduction of food or an underlying intervention to increase supply on wildlife may take several years to be discovered. It follows that, when inadequate food supply/stocks affects population maintenance, providing supplemental food should be considered for species conservation, especially for threatened species and/or at critical life history periods (Piersma and Baker, 2000; Ewen et al., 2015).

Supplemental feeding can mitigate food shortages within a short period and thus improve the health of animals (Robb et al., 2008a). This

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increases survival (Brittingham and Temple, 1988) and, indirectly, reproductive success rate (Castro et al., 2003; Robb et al., 2008b). Supplemental feeding, especially of garden birds, has become a widespread public activity and a common form of human–wildlife interaction in many western countries (Jones, 2018). This contributes to the pleasure and an increasing "biological awareness" of citizens (Reynolds et al., 2017; Jones, 2018).

Supplemental feeding, however, can have undesirable negative effects (Robb et al., 2008a; Jones, 2018). Supplemental food can cause concentrations of animals at the feeding sites, which increases intraspecific and interspecific contact and thus infectious disease risks (Lawson et al., 2012; Adelman et al., 2015; Wilcoxen et al., 2015; Murray et al., 2016). Supplemental food with insufficient nutritional quality might result in malnutrition and harm the physiology and health of the conservation targets (Ishigame et al., 2006; Raubenheimer and Simpson, 2006). Supplemental feeding can affect offspring sex ratio and increase the risks of stochastic fluctuations in the sex ratio in small populations (Clout et al., 2002). Feeding can affect the distribution, migration (Plummer et al., 2015; Masatomi and Masatomi, 2018), and dispersal of populations (López-López et al., 2004; Robb et al., 2008a; Oro et al., 2013). Different responses among species to supplemental food can alter interspecific relationship and community structure and cause cascading effects on the ecosystem (Fuller et al., 2008; Oro et al., 2013; Galbraith et al., 2015; Plummer et al., 2019). Because supplemental feeding has multiple direct and indirect effects on populations, communities, and ecosystems (Jones and Reynolds, 2008; Robb et al., 2008a; Jones, 2018), to achieve conservation objectives while minimizing adverse effects, supplemental feeding must be well designed. The present study argues through a case of supplemental feeding to help conserve a threatened migratory bird at an important staging site during migration from nonbreeding to breeding grounds.

Long-distance migratory birds usually require one or more staging sites with rich food for fuel deposition along their flyway (Warnock, 2010). Food conditions at refuelling sites determine fuel deposition (Rakhimberdiev et al., 2018), which can not only affect subsequent survival but also the performance after arrival at the migration destination (Smith and Moore, 2003; Morrison et al., 2007). Over the past several decades, habitat loss and degradation at stopover sites has caused serious food shortages and has thereby threatened many migratory species (Piersma et al., 2016; Cohen et al., 2017). In the East Asian-Australasian Flyway (EAAF), dramatic loss of tideland by land claim in the Yellow Sea (Murray et al., 2014; Chen et al., 2019), which contains critical refuelling sites for millions of migratory shorebirds (Barter, 2002), has caused rapid population declines in many shorebird species (Hua et al., 2015; Melville et al., 2016; Piersma et al., 2016; Studds et al., 2017). Meanwhile, the food shortage caused by habitat degradation along EAAF has attracted people's attention due to long-term ground monitoring in recent years (Zhang et al., 2018, 2019), which also have an negative effect on the survival and reproduction of migratory shorebirds (Piersma et al., 2016). Supplemental food for migratory birds at critical refuelling sites may mitigate the adverse effects of habitat loss and food shortage. This is the first case where supplemental feeding has been applied at a shorebird staging site. Because migratory shorebirds concentrate in large groups and stay for short periods at staging sites (e.g. Chan et al., 2019), it is necessary to provide enough food at the right time to match the migratory schedule. In addition, most supplemental feeding practices have targeted terrestrial animals rather than shorebirds in tidally structured marine areas which eat extensive macrobenthic foods.

Supplemental feeding for species conservation requires comprehensive planning (Ewen et al., 2015). As a trade-off among different scenarios (including the option 'no feeding'), supplemental feeding should achieve the maximum outcomes for the conservation of the targeted species and the minimum negative effects on other species and the environment. Based on supplemental feeding practiced over the past decades, we suggest that food supplementation for species conservation benefits from a three-step framework: (1) determining whether supplemental feeding is required; (2) designing and implementing supplemental feeding; and (3) evaluating the effectiveness of supplemental feeding. Working within this framework, in 2018 we provided supplemental food for great knots (*Calidris tenuirostris*), an endangered migratory shorebird species, at its critical refuelling site (Yalu Jiang estuarine wetland) in the Northern Yellow Sea, China, during northward migration (Fig. 1). The framework and the feeding practice may help guide supplemental feeding in a wide range of species in the future.

2. Framework for supplemental feeding

2.1. Step 1: determining whether supplemental feeding is required

Before supplemental feeding is initiated, it is necessary to assess the nature of the food shortage (Ewen et al., 2015). Severe weather conditions, such as snowfall in winter or drought in summer, can make it difficult for animals to obtain sufficient food for survival (Davidson, 1981). However, animals can adjust their physiology, ecology, and behaviour to adapt to seasonal food shortage (Piersma and van Gils, 2011). For example, many animals deposit large amounts of fuel in the form of fat before the season of food shortage (Davidson, 1981). Some animals store food and can use such food stores at times of scarcity. Other animals can avoid food shortage by moving away, probably the basic ecological cause of seasonal migration (Winkler et al., 2016). Moreover, although food shortage increases mortality, populations will recover or keep steady if environmental conditions improve in the subsequent seasons (Rakhimberdiev et al., 2015). Understanding the behaviour and ecology of wildlife is helpful for predicting the potential effects of food shortage.

Managers should consider whether there are alternatives to supplemental feeding (Ewen et al., 2015). For example, the population of a threatened species may be more effectively assisted by providing high-quality habitats with rich natural food than by directly providing supplemental food. The decision as to whether to provide supplemental food should be based on an assessment of both the positive and negative effects of all possible scenarios. If food shortage is temporary or reversible, supplementary feeding is not recommended.

2.2. Step 2: designing and implementing supplemental feeding

2.2.1. What to feed?

Although the increasing availability of commercial products makes it convenient to obtain supplemental food (Plummer et al., 2019), the best food is of course the natural food of the target animals (for review see Piersma, 2012). Collecting natural food, however, is generally difficult. If commercial food is selected, its nutrient content should be similar to that of the natural food. Providing food with the appropriate nutritional qualities is particularly important for feeding plans. It is also necessary to consider the possible effects of supplemental food on the environment, especially when the food consists of living organisms. The food remaining at the feeding stations or taken away by animals to nearby areas could negatively affect the local environment.

2.2.2. Where to do the supplemental feeding?

As foraging at unnatural sites may cause changes in the morphological and behavioural traits of animals (Piersma and van Gils, 2011; Bosse et al., 2017), feeding stations should be located at natural foraging sites of the target animals. Thus, the making available of food should be inspired by the foraging habits of the target animals (e.g., foraging in groups or territorial). Some animals have adapted to human activities; they can be fed near human dwelling places, thus providing opportunities for public education (McGeehan, 2005; Jones, 2018). For those species that are sensitive to human disturbance, however, feeding stations should be located to avoid human activities as much as possible.

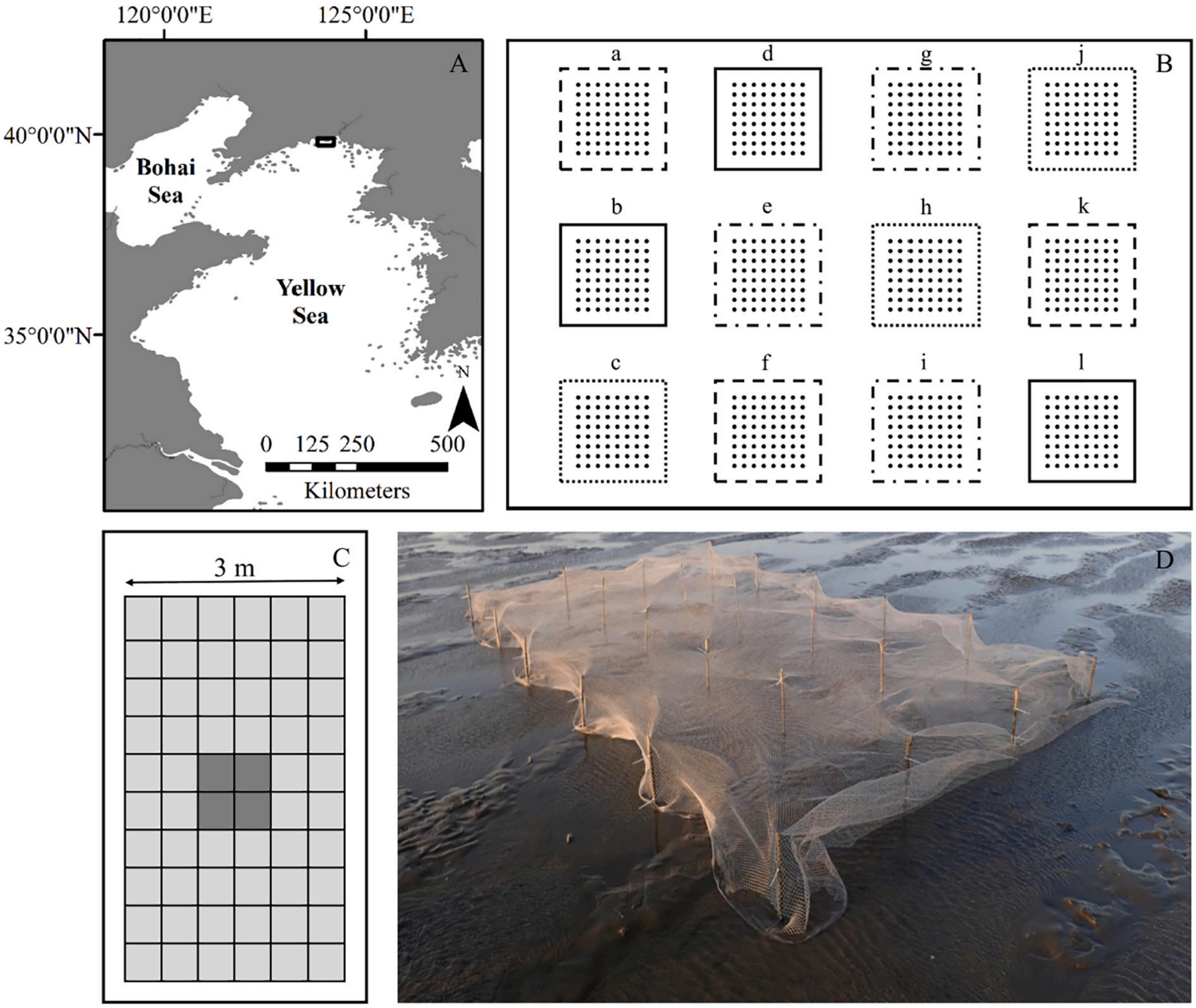

Fig. 1. Location of the Yalu Jiang estuary wetland in the Yellow Sea (A); layout of the feeding station with 3 high-density feeding zones (surrounded with solid lines), 3 medium-density feeding zones (surrounded with dashed lines), 3 low-density feeding zones (dash-dotted lines), and 3 control zones (surrounded with dotted lines) on the tideland at the Yalu Jiang estuary wetland (B). Each of the feeding zones and control zones was 200 m × 200 m. To verify whether living clams would move around and colonize areas outside the plots and to prevent the overestimation of the amount of food consumed by great knots, we designated nine 3 × 5 m '*P. laevis* spread sites' near the feeding zones to detect the spread of *P. laevis* (C & D). *P. laevis* was placed in a 1 m × 1 m area in the center of each spread site (dark grey area in C).

2.2.3. *When to feed?*

The feeding time should be selected to match the daily feeding schedule of the targeted species. Because many species use similar foods, a mismatch between feeding time and foraging time of the conservation target may cause the supplemental food to be largely consumed by other animals.

2.2.4. *How much to feed?*

Providing too much food will needlessly increase the cost for food and labour. In addition, extra food that remains unconsumed may have detrimental environmental effects. Therefore, the total amount of supplemental food, the amount of food to be fed each time, and the duration of the feeding period should be determined according to the biology of the conservation target.

2.3. *Step 3: evaluating the effectiveness of supplemental feeding*

An evaluation of the effectiveness of supplemental feeding may suggest if and how a project should be modified and improved (Armstrong and Perrott, 2000). This will also inform future projects. The ultimate goal of supplemental feeding is generally to maintain a stable population or to increase the population of a threatened species. However, the dynamic of a population is difficult to assess within a short period. Rather than evaluating population dynamics, researchers can assess the indices related to individual fitness (such as behaviour, body condition, home range size, and survival or breeding success rate).

The effectiveness of feeding can also be evaluated according to food use, such as the number of individuals that use the supplemental food, the total amount of food used, and the efficiency of food use; the latter variable can be determined by comparing feeding and no-feeding zones, feeding and no-feeding periods, or different feeding scenarios (Armstrong and Perrott, 2000; Chauvenet et al., 2012). As mentioned earlier, feeding may have unexpected consequences. Such as, supplemental feeding notably increased animal density and crowding (Murray et al., 2016), which could increase transmission of virulent pathogens (Wilcoxen et al., 2015; Murray et al., 2016). Even if certain pathogens have minimal fitness impacts on the target hosts themselves, greater infection prevalence (e.g., from high population density, or from improved immune function that improves tolerance to infection) could promote spillover risks to other species in the region (Adelman et al., 2015; Wilcoxen et al., 2015). Recognizing both the expected and unexpected consequences requires an integrative analysis of the responses of the conservation target and the effects on non-target organisms and the environment.

3. An example: the feeding of endangered great knots at their stopover site

The great knot is an endemic shorebird species in the EAAF. It breeds on mountain tundra in eastern Siberia and mainly stays in northwest Australia during the nonbreeding season (Tomkovich, 1997; Lisovski et al., 2016). The great knot is a intertidal molluscivore specialist outside the breeding period. The dramatic loss of intertidal habitat by land claims in the Yellow Sea region (Murray et al., 2014; Piersma et al., 2016; Chen et al., 2019), the critical habitats on which great knots depend for fuel deposition during migration (Chan et al., 2019), has caused a rapid population decline over the past two decades (~5.1% annually, Studds et al., 2017). In 2016 great knots were listed as endangered by the IUCN Red List (BirdLife International, 2019).

Supporting about 50,000 individuals at migration peaks (about 15% of the global population), the Yalu Jiang wetland in the North Yellow Sea is the most important refuelling site for great knots during northward migration (Ma et al., 2013; Choi et al., 2015). During the staging period, on the basis of substantial amounts of consumed food, great knots deposit a large amount of fuel, i.e. double their body mass, before departure to their breeding grounds (Ma et al., 2013). *Potamocorbula laevis*, a small bivalve that was abundant on the intertidal flats at Yalu Jiang until recently, was the most important food for knots, comprising about 95% of the total amount of food consumed (Choi et al., 2017). In recent years, however, the density of *P. laevis* has dramatically declined (Zhang et al., 2018). This decline has resulted in a decrease in the fuel deposition rate of the great knots at stopover sites (Zhang et al., 2019) and is likely to negatively cascade into breeding performance in the upcoming season (Senner et al., 2015). Supplemental feeding will increase fuel deposition rate and thus help maintain their population.

3.1. Methods

According to the three-step framework, we supplemented the food available for great knots at Yalu Jiang in the spring of 2018 (Table 1). Before implementation of supplemental feeding, we held two demonstration meetings on the supplemental feeding activity with invited experts in bird ecology, coastal macrobenthos, wetland ecology, and conservation biology. The meetings focused on discussing the necessity, feasibility, and potential effects of the supplemental feeding.

3.1.1. Is supplemental food necessary for the great knots?

To determine whether it was necessary to provide supplemental food for great knots at Yalu Jiang, we surveyed the intertidal bivalve stocks available to the great knots and measured food intake rate of the early arriving birds. Using simple energetic models, we also estimated whether great knots should be able to deposit enough fuel at Yalu Jiang in the absence of supplemental feeding.

To measure available food stocks, we sampled the macrobenthic invertebrates along 16 transects that were separated by at least 500 m in late March of 2018; samples were collected at a total of 104 locations on these transects (see details in Zhang et al., 2018). One core sample (diameter 15.5 cm, depth 5 cm) was collected at each sampling location. The samples were washed on a 0.5-mm sieve. With bill length of great knots of about 45 mm, we considered the macrobenthos from the top 5 cm of sediment to be the harvestable food fraction (Zhang et al., 2018). The hard-shelled bivalves, gastropods, and crustaceans collected on the sieve were sealed in plastic bags and frozen, but soft-bodied organisms were preserved in 75% ethanol. In the laboratory, we identified all organisms to the finest practicable taxonomic level and measured their length (to 0.01 mm) using a dissecting microscope. We estimated ash-free dry mass (AFDM, an index of the amount of fuel available to the birds) for each taxonomic group according to established regression models between AFDM and body length (See details in Zhang et al., 2018, 2019).

Table 1
The three-step framework for food supplementation and an example involving the feeding of great knots at a stopover site.

Step	Major questions	Answers
1) Determine whether supplemental feeding is required	a) Is the natural food insufficient? b) What are the effects of food shortage? c) Are there alternatives to supplemental feeding?	a) The main natural food for birds had decreased by > 95%. b) Decreased foraging efficiency cannot meet the requirement of fuel deposition for migration flight, which adversely affects the survival and breeding. c) Birds unlikely to move to other stopover sites.
2) Design and implement food supplementation	a) What food to feed? b) How much food to feed? c) Where to feed? d) When to feed? e) What are the environmental effects of feeding?	a) *Potamocorbula laevis*, the major natural food for birds, is a widespread species that occurs at both YLE and the source site in Bohai. It is easy to obtain locally. b) Determine the amount of food required according to the food use by birds. c) Place *P. laevis* on the tideland, the foraging site for birds, according to its historical density. d) During high tide when food transportation and spreading are convenient. Birds can find food after the tide falls. e) The *P. laevis* used to feeding comes from the subtidal zone, which will not reduce the foraging opportunities of shorebirds staging there; Dead *P. laevis* due to the long-distance transportation would be dispersed by tidal movement; Compared with the consumption for aquaculture, the amount of feeding is very small thus will not affect other species at the source site.
3) Evaluate the effectiveness of food supplementation	a) How many animals used the food? b) How much food was used? c) How did the animals benefit? d) What was the effect on other animals?	a) There were 5842 ± 4070 birds foraging daily; the peak number (13410) accounted for 47.6% of the total number of great knots at YLE. b) Nearly 90% (116 t) of the supplemental food was used by birds. c) Food intake rate increased by 4.2 times during the feeding period. d) Other birds, such as bar-tailed godwits, also benefitted from the supplemental food.

To assess the fuel deposition rate of great knots in the experimental situation, we recorded the behaviour of foraging great knots with a digital video camera connected to a ×20–60 telescope. A focal bird was selected at random from a flock of foraging birds. Each record lasted for at least 5 min. We used BORIS (Friard and Gamba, 2016) to quantify the time a bird spent on different behaviours and to identify the prey and prey size (estimated as a proportion of bill length) consumed by birds. Based on the species and numbers of prey taken by the focal birds and the relationship between prey size and prey AFDM (Zhang et al., 2019), we calculated the biomass intake rate of the birds in mg AFDM per second. Based on staging time, the total amount of fuel that birds are required to deposit, and the fuel deposition rate at Yalu Jiang, we estimated the required daily foraging time of great knots as:

$$\text{The required daily foraging time} = \text{NEI} \times 1000/(3600 \times \text{IR} \times \text{EV} \times \text{AE})$$

Here, NEI is the required amount of daily net energy intake (232.64 kJ, Zhang et al., 2019), IR is food intake rate (mg AFDM/s), EV represents the energetic value of 1 g AFDM (22 kJ, Chambers and Milne, 1975), and AE is the assimilation efficiency (0.75, Kersten and Piersma, 1987).

We assessed whether birds can achieve the required daily gain in body mass at Yalu Jiang necessary to migrate by comparing the required daily foraging time and available daily foraging time during stopover. When consuming natural foods at Yalu Jiang, the average available foraging time of great knots on the intertidal areas in 2018 was estimated to be 8 and 10 h per day during spring and neap tide, respectively. We assumed that the intake rates would be similar in daylight and at night (Santiago-Quesada et al., 2014, and see evidence for great knots and related species in Rogers et al., 2006; Cohen et al., 2011).

3.1.2. How to feed the great knots?

3.1.2.1. What to feed the great knots?. We used live *P. laevis* as the supplemental food for several reasons. First, when available, *P. laevis* has been shown to make up much of the diet of great knots (Choi et al., 2017). When eating this food, great knots swallow the clam whole and crush the thin shell in their gizzard (Yang et al., 2013). Other clams are either too large to be swallowed or have shells that are too hard to be crushed in the gizzard (Zhang et al., 2019). Second, because *P. laevis* has been a dominant component of the intertidal benthic community at Yalu Jiang (Choi et al., 2014), introducing *P. laevis* as supplemental food on the intertidal area represents something 'normal'. Third, *P. laevis* is commonly present, widely cultivated (Yang et al., 2016), and therefore can be relatively 'safely' collected, without further detrimental effects on the local environment.

3.1.2.2. Where to feed the great knots?. Foraging great knots follow the tideline, so feeding stations were established on the intertidal zone where *P. laevis* naturally occurred and where great knots commonly foraged. As a consequence, even if some of the supplied *P. laevis* were not eaten by the birds, the surviving *P. laevis* could settle in the intertidal sediments and contribute to the recovery of the local *P. laevis* population.

3.1.2.3. When to feed the great knots?. Great knots remain at Yalu Jiang for about 1.5 months on northward migration. Numbers of great knots are highest from mid-April to mid-May (Ma et al., 2013). Providing supplemental food many times during this period would enable birds to obtain food throughout the staging period. We purchased *P. laevis* that were collected in the subtidal flat by local fishermen. A fishing boat was used to transport the *P. laevis* to pre-determined feeding areas for release during the high tide of the spring tide series (Fig. 2). Bamboo poles with different colored flags marked the boundaries of the feeding stations. A GPS track of the boat confirmed that *P. laevis* were correctly distributed on the tideland. According to the staging period of great knots and the time when the local fishermen harvested *P. laevis*, we carried out a total of eight food supplements. The dates were as follows: 15 April, 18 April, 20 April, 21 April, 22 April, 23 April, 1 May, and 4 May.

3.1.2.4. How much to feed the great knots?. To meet the requirement of energy accumulation during the staging period at Yalu Jiang, each great knot was assumed to consume 188 g fresh mass (including shell material) of *P. laevis* per 24 h (Zhang et al., 2019). With an average staging duration of 31 days (Ma et al., 2013), each bird would consume 5.8 kg fresh mass of *P. laevis*. Multiplied by the estimated numbers of staging great knots over the previous three years (i.e. 35,380) (Choi et al., 2017; Zhang et al., 2018), a total of 206,000 kg fresh mass *P. laevis* would be required.

Twelve plots (3 rows and 4 columns, 200 m × 200 m for each zone)

Fig. 2. Transport the living *Potamocorbula laevis* from refrigerator truck to the boat (upper left) and spreading the clams at a feeding zone during high tide (upper right) (photo: Shoudong Zhang). Foraging great knots at a feeding zone. Some bar-tailed godwits are also foraging (photo: Qingquan Bai).

were designated as the feeding stations in the intertidal zone (Fig. 1). To compare the responses of birds to different food densities, three zones in each row were randomly selected as high (~1000 ind/m^2), medium (~200 ind/m^2), and low density (~40 ind/m^2) feeding zones (with added food); and another one as control zone (without added food) (Fig. 1). The density of *P. laevis* in the high-density feeding zones was similar to the natural *P. laevis* density at Yalu Jiang in 2011–2012 (Zhang et al., 2018). Clams was spread onto the three feeding zones at one of the three rows in turn for each feeding. Adjacent zones were separated by 200 m. To count birds and record bird behaviours without disturbance, observers walked the areas between zones. The bamboo poles with different colored flags at the four corners of each zone used during the release of the *P. laevis* also served as markers during low tide.

3.1.3. Evaluating feeding effectiveness

The effectiveness of supplemental food was evaluated on the basis of (1) the amount of food consumed, (2) the number of foraging great knots in the supplementation zones, (3) their rate of food intake, and (4) body mass change (reflecting fuel deposition) of great knots during stopover. Macrobenthos were sampled at the feeding and control zones before and after food was provided. In each zone, a total of 64 core samples (diameter 15.5 cm, depth 5 cm) were collected at 25-m intervals and were then washed on a 0.5-mm sieve. Macrobenthos were surveyed every day until most of the *P. laevis* were consumed by the great knots in the feeding zones (5 days). The methods were the same as mentioned above (Section 3.1.1).

Great knots and other birds were counted at their roosting sites during the high spring tide at Yalu Jiang as part of the routine shorebird monitoring program from late March to mid-May in 2018 (Zhang et al., 2018). We also determined the species and number of shorebirds foraging at the feeding zones every day following the addition of supplemental food (from April 15 to May 8, suspended on April 22 and April 30 due to bad weather, Fig. 3). Least squares linear regressions were used to assess the relationship between the number of great knots and *P. laevis* density in the feeding zones.

Behaviours of great knots were recorded at the feeding zones (177 records) and the control zones (128 records) using a digital video camera connected to a ×20–60 telescope, as noted above. According to the proportion of great knot numbers in the feeding zones with different food density, the number of video records taken each day was allocated between the feeding zones based approximately on the proportion of great knots present in each zone with different food density – the higher the food density the greater the number of great knots, and thus the higher number of videos recorded. The food intake rate of great knots in all plots of the same density class was similar (Zhang et al., unpublished data), so we combined the video records for each density class. To ascertain prey species and size, we collected droppings of great knots at the feeding zones (1463 droppings) and control zones (550 droppings) after the birds had flown away. Using video records, we calculated the fuel intake rate and estimated the daily foraging time that great knots required to deposit sufficient fuel to support the next stage of their migratory flight, this being done for each of the feeding and control zones (Zhang et al., 2019).

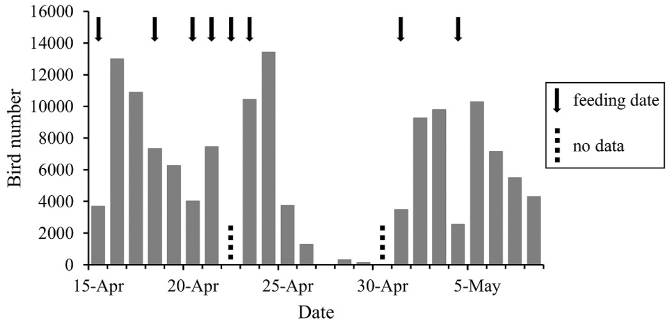

Fig. 3. Total numbers of great knots at the feeding stations (i.e. the sum of all feeding zones) during the feeding period from 15 April to 8 May 2018. The arrows show the feeding dates. Bird counts were not conducted on April 22 and 30 due to bad weather conditions.

To detect how much supplemental food was consumed by birds, we determined the numbers of *P. laevis* at the feeding zones for five consecutive days after food was provided until *P. laevis* numbers were <5 ind/m^2 (i.e., when 90–99% of supplemental food had been consumed).

If living clams would move around and colonize areas outside the plots, the amount of food consumed would be overestimated. To detect the spread of *P. laevis*, we designated nine 3 × 5 m '*P. laevis* spread sites' near the feeding zones. About 2000 individuals of *P. laevis* were evenly placed in a 1 × 1 m area in each spread site. Bamboo poles (30 cm long) were inserted into the surrounding substrate at 1-m intervals. Fishing nets were fixed on the tops of the bamboo poles to cover each 3 × 5 m spread site. The nets prevented birds from feeding but did not affect the tidal flows (Fig. 1). Core samples (diameter 15.5 cm, depth 5 cm) were collected at 0.5-m intervals throughout each spread site, including four samples that were collected in the central area where the clams had been placed. The core samples were washed on a 0.5-mm sieve, and the collected *P. laevis* were counted and then returned to their original location in the spread site. The spread sites were sampled for three consecutive days following supplementation. We compared the numbers of *P. laevis* on the first and the second day after *P. laevis* was released with the number on the day when *P. laevis* was released to evaluate the percentage of *P. laevis* that settled (i.e., that remained in place). Because no *P. laevis* was recorded in any spread site before supplemental food was provided, we ignored the influence of naturally distributed *P. laevis* on the results. On the first day after *P. laevis* was placed, 90.8 ± 3.2% (n = 9) of the placed *P. laevis* were collected in the spread sites; 88.3 ± 3.2% were collected in the centers of the sites where *P. laevis* was placed and 2.5 ± 1.8% were collected in the surrounding area within 1 m of the placement location. On the second day after *P. laevis* was placed, 90.2 ± 3.3% (n = 9) of the placed *P. laevis* were collected in the spread sites; 86.7 ± 5.4% were collected in the centers of the sites where *P. laevis* was placed and 3.5 ± 4.4% were collected in the surrounding area within 1 m of the placement location. This suggested that 9% of the added *P. laevis* may be lost on the first day (field observations suggested that most of these were dead individuals that were washed away with tide-water), and the remaining individuals soon settled and rarely moved on the tideland. In the diffusion experiment, re-surveys only occurred within 2 days after *P. laevis* drops for the following reasons: (1) there were only about 5% of the food was left on the third day after feeding through the two feedings on 15 and 18 April, (2) and the recollection rate on the second day of the diffusion experiment was > 99% compared to the first day, and (3) the maximum spreading distance was shorter than 1.5 m, this distance could be ignored in the 200 m × 200 m feeding area. Because the feeding station covered a large area (200 m × 200 m for each zone) and the feeding lasted for only a short period (total 20 days), we have assumed that 91% of the added *P. laevis* were available to the birds.

It should be considered that the risk of pathogen transmission caused by animal density increased in the supplementary feeding project. Great knots often forage in flocks during non-breeding seasons (Tulp and de Goeij, 1994; Lisovski et al., 2016). In 2011 and 2012, when food store was abundant on the mudflat at Yalu Jiang, great knots usually formed large foraging flock (bird number can reach 10,000 to 30,000, Choi et al., 2017). In addition, great knots usually roost in dense flocks at high tide (the number of great knots at one high tide roost can reach about 44,000) during spring tides at Yalu Jiang (Choi et al., 2015). The density of great knots in the high-density feeding area was similar to the density in 2011 and 2012, which was much lower than the density at the high tide roost; furthermore, the intertidal flats where the birds foraged are regularly cleansed by tidal inundation. Therefore, we did not consider the potential pathogen transmission due to the increase in bird density caused by supplementary feeding in this study. However, it should be considered when feeding other species, especially in terrestrial locations.

To clarify the function of supplemental feeding for fuel deposition of the great knots, we used linear regression to detect the changes of daily average body mass, an indicator of fuel deposition at population level, during stopover in 2010–2012 (with abundant food) and in 2018 (year of food shortage). The daily average body mass of great knots came from 327 individuals captured in 2010–2012 (Ma et al., 2013) and 153 individuals drowned accidentally in the fishing nets set on the intertidal zone in 2018 (Zhang et al., 2019).

Statistical analyses were performed in SPSS 20.0, and the significance level was set at 0.05.

3.2. Results

3.2.1. The necessity of supplemental feeding for great knots

In late March of 2018, in the Yalu Jiang intertidal flats, the available food stocks suitable for great knots amounted to 0.73 ± 1.91 g AFDM/m^2 ($n = 104$). During this period the mean food intake rate of great knots was 0.28 ± 0.39 mg AFDM/s ($n = 49$). To deposit enough fuel for the next leg of their migratory flight, the birds would need to forage for at least 14 h each day. This is longer than the available foraging time (8–10 h per day). As a consequence, the food intake rate would not enable great knots to deposit sufficient fuel for the next leg of their migratory flight.

All of the invited experts agreed with the authors that the food shortage at Yalu Jiang would aggravate the threats to the endangered great knots and would likely cause a further decline in their population size. As a consequence, we decided that supplemental food was needed to maintain the population of great knots. All of the invited experts approved of using *P. laevis* as the supplemental food of choice and that the use of *P. laevis* was unlikely to have significant adverse effects on the local environment. According to the information provided by the *P. laevis* supplier, *P. laevis* used for supplemental feeding are < 5% of the locally available subtidal stock, and these *P. laevis* were originally used for food production and was diverted for the conservation feeding. Therefore, it could not affect the long-term replenishment of *P. laevis* and predators in the subtidal zone. The feeding was carried out by the volunteers from the Happy Dedicated Volunteer Station in Dandong, and the local tideland managers were happy to provide an area to feed the birds.

3.2.2. Implementation of supplemental feeding of great knots

Due to funding constraints and limitations of suitable tidal conditions for distributing clams, we were only able to provide 129,000 kg fresh mass of *P. laevis* rather than the calculated requirement of 228,000 kg (including the estimated losses during supplementation of 10%). This amount was distributed during eight days (16.1 ± 7.0 t per day, $n = 8$) between 15 April and 4 May at intervals of 0–3 days (Fig. 3). During the neap tides from 24 to 30 April, tidal heights at high tide were insufficient to allow access by the fishing boats, so feeding was suspended (Fig. 3).

3.2.3. Effectiveness of great knot feeding

3.2.3.1. Changes in bird numbers and food density at feeding zones.

Large numbers of great knots were attracted to the feeding zones soon after *P. laevis* was added. During the supplemental feeding period, the total number of great knots per day was 6100 ± 2823 ($n = 22$) across all the

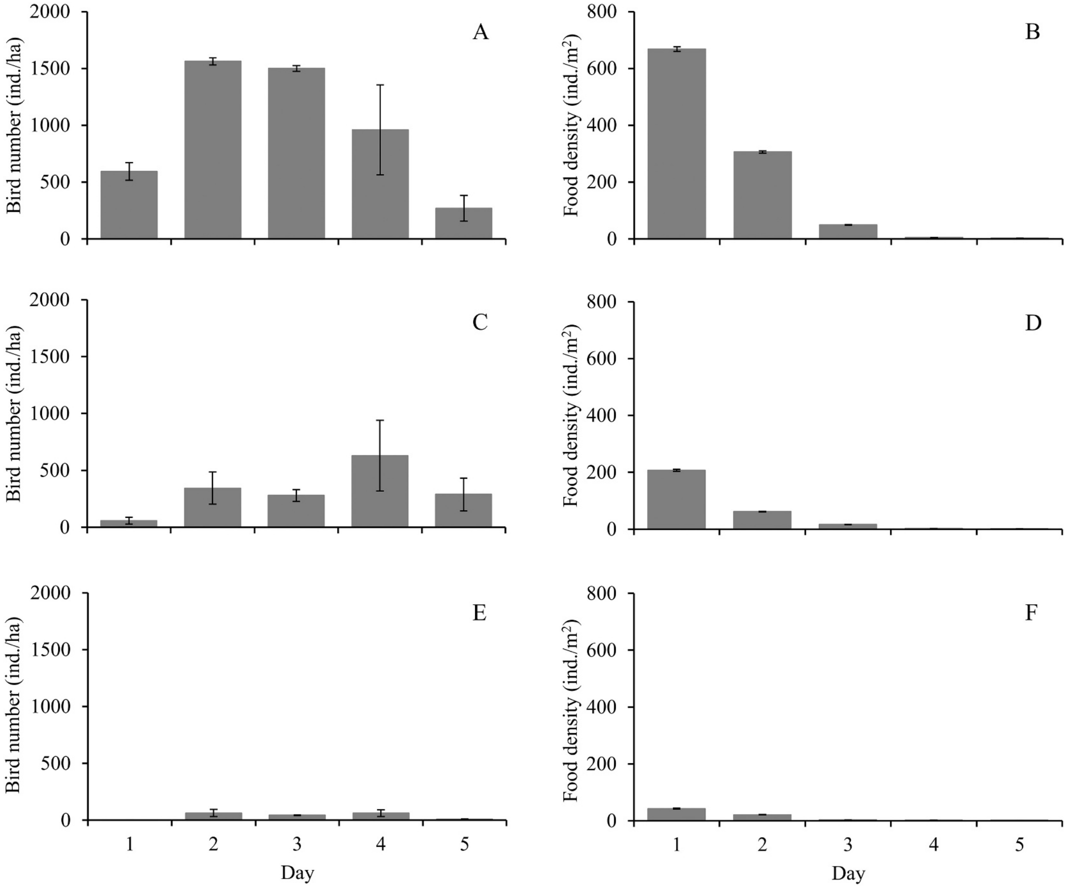

Fig. 4. Number of great knots per ha (A, C, E) and food density (*P. laevis*) (B, D, F) in the feeding zones with high density (A & B), medium density (C & D), and low density (E & F) food. *P. laevis* was added on day 1. Values are means ± SD. Note different scales.

plots. The highest number (13410) accounted for 48% of the highest total count of great knots at the Yalu Jiang wetland (Fig. 3). Among the three feeding zones with different food densities, most birds ($> 80\%$) concentrated in the high-density feeding zones, with fewer birds occurring in the low-density feeding zones (Fig. 4). In the high-density feeding zones, the density of great knots peaked at 1562 ± 62 ind/ha on the second day, i.e., 1 day after *P. laevis* was added (Fig. 4). Some bar-tailed godwits (*Limosa lapponica*) were also attracted to the supplemented feeding stations/plots (Fig. 2). The largest number of bar-tailed godwits recorded on one day during the feeding period was 5170 birds (total of all the zones).

During the feeding period, clam densities decreased in all three food density zones (Fig. 4). The initial densities of *P. laevis* were 667.9 ± 8.4, 207.5 ± 463.4, and 42.5 ± 181.6 ind/m^2 in the high-, medium-, and low-density feeding zones, respectively. More than 90% of the clams had disappeared by the third day after supplementation. The density of *P. laevis* dropped to 3.3 ± 0.1, 0.8 ± 6.6, and 0.4 ± 4.7 ind/m^2 in the high-, medium-, and low-density feeding zones, respectively, on the fifth day after feeding (Fig. 4). All the data in the analysis are aggregates from multiple feeding events. The number of great knots per feeding zone was significantly correlated with the density of *P. laevis* at that feeding zone ($r = 0.66$, $P < 0.001$, $n = 66$). Given that 90% of the supplemental *P. laevis* was available to the birds in the feeding zones, the results indicate that nearly all (99.8%) of the available supplemented *P. laevis* were removed from the feeding zones by 10 May 2018. Thus, a total of 90% (116 t, calculated as 129 t × 90.2% × 99.8%) of the supplemental *P. laevis* were consumed, mainly by the great knots.

3.2.3.2. Food use by great knots. In the control zones great knots mainly fed on *Umbonium thomasi*, *Lingula natine*, and *Ogyrides orientalis*, but in the supplemented plots they only ate *P. laevis* (Table S1). The food intake rate per great knot was significantly higher in the high-density feeding zones (1.2 ± 0.9 mg AFDM/s, $n = 177$, including all the video records during the feeding periods) than in the control zones (0.3 ± 0.4 mg AFDM/s, $n = 128$, Mann-Whitney U tests, $P < 0.001$). To deposit enough fuel within the limited stopover period at Yalu Jiang for the next leg of their migratory flight, the great knots would have had to forage in the high-density supplementary feeding zones for 3.5 h per day. This is one third of the maximally available low tide foraging time at the sites of the supplemented plots.

The daily average body mass of great knots increased with date during stopover in 2010–2012 ($r = 0.73$, $P < 0.001$) and in 2018 ($r = 0.67$, $P < 0.001$). However, pre-departure body mass (20th May) was about 15 g lower in 2018 than that in 2010–2012 (Fig. 5).

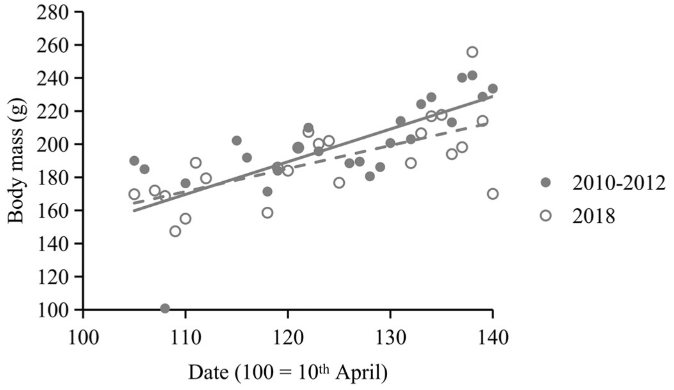

Fig. 5. Daily average body mass of the Great Knots staging at Yalu Jiang wetland in the spring of 2010–2012 (with abundant food, $n = 24$) and 2018 (year of food shortage, $n = 24$). The solid line and dashed line indicate the linear regression in 2010–2012 (body mass $= 1.97 \times$ date $- 47.30$) and in 2018 (body mass $= 1.39 \times$ date $+ 18.33$), respectively.

4. Discussion

As a management intervention, supplemental feeding is often controversial (Martínez-Abraín and Oro, 2013). However, like habitat restoration, reserve fencing, and predator control, supplemental feeding in some cases may be an important conservation measure. It could help when a short interval of food shortage threatens the survival of the animals of concern. Based on an integrated consideration of the necessity, feasibility and consequences, the three-step framework can help wildlife managers implement supplemental feeding and reduce any adverse effects. In the example described here (i.e., the supplemental feeding of migrating great knots at a critical refuelling site), tens of thousands of birds consumed the supplemental food (some 116 t of living *P. laevis*) and exhibited high foraging efficiency similar to that in early 2010s when natural food was superabundant (Choi et al., 2017). Although we have no direct data on the rate of fuel deposition and the contribution of supplementary food to population maintenance of great knots, the supplementary food clearly benefited this endangered species. To our knowledge, this is the first report of successful supplemental feeding of a migratory shorebird at a staging/refuelling site.

Migratory shorebirds often use the same refuelling sites year after year (Verhoeven et al., 2020) and are unlikely to change refuelling sites when facing food shortage, probably due to the time constraints of the migratory journey (Ke et al., 2019). The Saemangeum estuary in South Korea, for example, was previously the most important refuelling site for great knots during northward migration, supporting over 20% of the global population. Large-scale land claim destroyed this area in 2006 and great knots displaced from Saemangeum did not relocate to other sites nearby, resulting in a sharp decline in the global population (Moores et al., 2016). Because habitat loss has been common in the Yellow Sea, there simply may be no alternative sites suitable for refuelling in this region (Zhang et al., 2018). As a relatively long-lived bird, populations will not bounce back rapidly following a decline (Piersma and Baker, 2000). For these reasons, when food shortages are evident at a critical refuelling site, food supplementation seems an appropriate conservation/management option.

Supplemented food can of course be consumed by others than the target species. In addition to being the major food for great knots at Yalu Jiang, *P. laevis* was also the major food for many other shorebirds. *P. laevis* accounted for 65% of the food of bar-tailed godwits, one of the dominant shorebirds (its peak number was >60,000 birds) at Yalu Jiang (Choi et al., 2017). We found that many bar-tailed godwits consumed the supplemental food in our feeding zones, suggesting that our estimates of the supplemental food required to meet the requirement of great knots should account for the supplemental food consumed by bar-tailed godwits.

However, due to the restrictions of funding, transportation of *P. laevis*, and tidal conditions, we were only able to conduct supplementary feeding during part of the entire stopover period and we provided only about half the amount of food that the great knots required. We found that body mass of great knots at departure was lighter, suggesting lower fuel deposition, in 2018 than that in the early 2010s when food was superabundant at Yalu Jiang. Moreover, in the early 2010s, after arrival great knots stayed put at Yalu Jiang until their departure to the breeding grounds (Ma et al., 2013). However, a marked great knot was recorded making two round trip flights between Yalu Jiang and Bohai Bay (500 km away) in spring 2018 (DSM, personal communication). This suggests that some individuals failing to find high quality foraging sites may try to go elsewhere. The anecdote also suggests that supplemental food reduced the food shortage, but did not fully meet the requirement of the great knots.

Although supplemental feeding can reduce a food shortage within a short period, the long-term conservation of the target species requires the combining of supplemental feeding with other conservation measures. For example, if the food shortage is caused by habitat loss and degradation, habitat restoration is required. At Yalu Jiang, food shortage for great knots does not seem to be a temporary problem. The densities of *P. laevis* have decreased since 2013 for unknown reasons (Zhang et al., 2018). In recent years, the peak number of great knots and bar-tailed godwits has declined, which may be closely related to the food decline (Choi et al., 2015; Zhang et al., 2018). It follows that researchers must determine the causes of the food decline in order to restore the natural population of *P. laevis* so that the tideland ecosystem can support great knots and other shorebirds.

Feeding might have some unexpected effects in the long-term, especially if the supplemental food is not the natural food of the target animals (Plummer et al., 2013; Bosse et al., 2017). Therefore, long-term monitoring of animal physiology, behaviour, and population characteristics are important for evaluating the feeding effects. However, this is challenging for great knots and other migratory birds that depend on multiple and remote regions for their annual life cycle. In this study, supplemental feeding was conducted in accordance with natural conditions, i.e., with respect to food type, foraging site, and food density, so as to avoid potential negative effects on the great knots and other birds. Although a small amount of dead *P. laevis* due to the long-distance transportation were spread in the feeding zones, they were quickly dispersed by the tidal water movements. In addition, since great knots gather in large groups to forage and rest, we did not consider the potential pathogen transmission due to the increase in bird density caused by supplementary feeding in this study. However, in the supplementary feeding activities for other groups, researchers need to quantify pathogen (such as viruses, ecto- and endo-parasites) infection or intensity as part of evaluation pre and post intervention.

In the future, the increasing frequency of extreme weather and the increasing range and intensity of human activities will increase the uncertainty of food availability for wildlife. As an effective management intervention that can work in a short period, supplemental feeding is likely to have an increasing role in species conservation, especially for those threatened species with small populations. The current report on a three-step framework combined with the example of great knots highlights the importance of supplemental feeding for in situ conservation.

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CRediT authorship contribution statement

SDZ, ZJM, and TP wrote the manuscript. SDZ analyzed the data. SDZ, QQB, DSM, and CCF contributed to sampling and laboratory experiments. ZJM, SDZ, DSM, QQB, and TP designed the study.

Declaration of competing interest

We declare that we have no conflicts of interest to this work, we do not have any commercial or associated interests that conflict with the submitted works, there are no part of the research has been published in any form elsewhere, the manuscript is not being considered for publication elsewhere while it is being considered for publication in Biological Conservation, and all sources of funding are acknowledged in the manuscript.

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to Biological Conservation.

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