

Diurnal and nocturnal feeding rate in Kentish plovers *Charadrius alexandrinus* on an intertidal flat as recorded by telescopic video systems

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Received: 19 April 2006 / Accepted: 3 October 2006 / Published online: 28 October 2006
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Abstract To elucidate the effects of light, site, temperature, time after emersion, and wind speed on foraging attempt rate (FAR) (attempts/unit time) and feeding success (FS) (captures/attempts) in the obligate visual foraging shorebird, Kentish plovers *Charadrius alexandrinus*, field observations were performed at a sandflat in Tokyo Bay, using a visible-light telescope camcorder during the day and a thermal infrared telescope camcorder at night. The re-analysis capability and frame-step replay of highly magnified video-images can contribute to accurate measurement of feeding behaviour over conventional focal observation techniques. Kentish plovers increased both FAR and FS in areas of high prey (polychaetes and crabs) density, resulting in a synergistic increase in feeding rate (captures/unit time). In areas of high prey abundance, FAR was higher at lower wind speed. FS increased with increasing time after emersion. Increasing temperatures induced a positive effect on FAR but a negative effect on FS. The effect of light on FAR was not observed; however, time-to-defecation occurrence was 2.2-fold shorter at night than during the day, indicating that feeding rate and FS are higher at night. These results are attributable to an increase in availability of cues due to higher nocturnal activity in polychaetes. Since available foraging time (emersion

time) at night was 1.7-fold longer than during the day in the present study period, Kentish plovers could capture 3.7-fold (2.2×1.7) more prey at night than during the day. Results from this study indicate that nocturnal feeding in overwintering plovers is not a compensation but a major foraging activity to meet their energy requirements.

Introduction

Animals that forage on hidden or mobile prey are bound to experience capture failure. In such foragers, feeding rate (number of captures per unit time) is determined by both foraging attempt rate (FAR) (number of attempts per unit time) and feeding success (FS) (captures/attempts). Thus, the breakdown of feeding rate into FAR and FS and subsequent separate investigation of extrinsic and intrinsic constraints on each component may be important for better understanding of the feeding ecology of relevant animals. In shorebirds, a number of studies on environmental constraints have been related to prey density (Goss-Custard 1970, 1977; Wilson 1990; Kalejta and Hockey 1994; Zharikov and Skilleter 2003; Lourenço et al. 2005). However, other environmental constraints have not yet been well studied (Pienkowski 1983a, b; McNeil et al. 1992; Turpie and Hockey 1993). In particular, the effect of light is important in the context of the biology of overwintering shorebirds in temperate regions, because diurnal feeding alone has been reported to be insufficient to balance energy budgets due to restriction of foraging time by short day-length (McNeil et al. 1992; Mouritsen 1994).

Communicated by S. Nishida, Tokyo.

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Extrinsic and intrinsic constraints on FAR include the frequency of cues to locate hidden prey and forager's ability to detect cues. For example, plovers on intertidal flats detect and capture prey by exploiting visual cues, including the brief-period surface activity of prey and outflow of water from the burrows (Pienkowski 1983c; Esselink and Zwarts 1989). The frequency of cues is dependent on prey activity in addition to prey density. Prey activity is influenced by ambient conditions, such as light, temperature, and tidal regime (e.g. Pienkowski 1983c; Yokoyama 1988; Deschênes et al. 2005). Plovers' ability to detect cues is also primarily related to light, wind, and rain (Pienkowski 1983a; Piersma 1987; McNeil et al. 1992). At night, visual acuity and sensitivity may be lower than during the day, although plovers have been reported to be morphologically and physiologically well-adapted to nocturnal visual foraging because of their large eyes and greater retinal visual sensitivity (Rojas de Azuaje et al. 1993, 1999; Thomas et al. 2006). Wind and rain can generate turbulence on the surface of standing water on sediments and act as "noise", interrupting visual cue detection by plovers.

Major constraints on FS include escape ability of mobile prey (Backwell et al. 1998; Hügler 2004) and, similarly to FAR, the frequency of cues arising from hidden prey. Since abundant cues provide foragers an opportunity for rigorous assessment, FS should be higher when the frequency of cues is higher. By increasing FS, foragers can save energy costs for foraging workload and attain efficient foraging, i.e. higher total net energy gain per unit energy expenditure. Such an adjustment of foraging behaviour would be an important part of strategy for foragers (Ydenberg and Hurd 1998).

Conventionally, the feeding behaviour of shorebirds is examined by focal observations using a spotting scope (20–60× optical magnification). However, given the evidence for microphagy in small shorebirds, which shows the size of their prey being down to millimeters (Mercier and Gaskin 1985) or even micrometers (Zwarts et al. 1990; Sutherland et al. 2000; Elner et al. 2005), the magnification of spotting scopes is often insufficient for in situ observations of FS in broad intertidal flats and wetlands. In addition, subjectivity and observational errors are inevitable in focal observations due to incapability of re-analysis. To overcome these problems, I introduced telescopic video systems in the present study.

Here I report on FAR and FS in overwintering Kentish plovers *Charadrius alexandrinus* (L.) at a sandflat in Tokyo Bay, Japan. The Kentish plover is an obligate visual forager and a common overwintering

Charadrii shorebird on intertidal flats around Japan. The study site supports up to 2000 dunlin *Calidris alpina* (L.) and up to 400–600 Kentish plover during an overwintering period. Using a generalized linear model (GLM) and the multimodel selection technique, I test the hypothesis that light, site, temperature, time after emersion, and wind speed affect the FAR and FS of Kentish plovers. Shorebirds overwintering on intertidal flats are excellent subjects for testing this hypothesis, because they experience drastic changes in environmental conditions within the tidal cycle. I predict that both FAR and FS should increase when the frequency of cues increases (e.g. at a high prey density site and at high temperatures) or detectability of cues increases (e.g. during the day and at low winds).

Methods

Study site

The study area, Banzu intertidal sandflat (35°24.8'N, 139°53.9'E), is located on the east coast of Tokyo Bay and covers an area of 7.6 km² (Fig. 1). Tides are semi-diurnal with amplitudes from 0.5 to 1.6 m. The slope of the seabed at the site is gentle (ca. 0.07 cm m⁻¹). The observation area has the highest elevation and consequently the longest sediment emersion time and

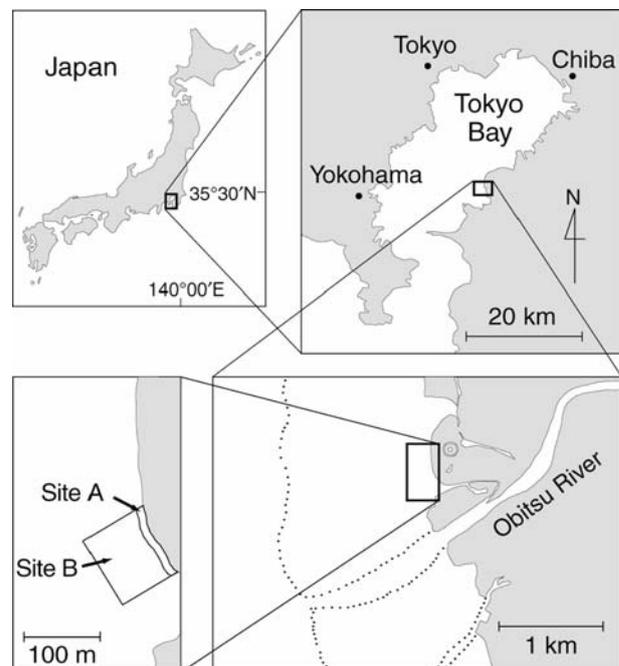


Fig. 1 Location of the study site (Banzu intertidal flat, Tokyo Bay, Japan). Dotted lines indicate the lowest tidal level

shorebird use time in the Banzu intertidal flat. There is no macro-vegetation on the observation area, although marsh plants, comprised mainly by the common reed *Phragmites australis* (Cav.), are present along the shore.

I defined two sites based on sediment characteristics: Site A was located along the edge of the shore (0–10 m away from the shore \times ca. 100 m along the shore), and Site B was 10–80 m away from the shore \times ca. 100 m along the shore. Sediments at both sites are characterized by well-sorted fine sand with a median grain size of 220–270 μm . However, Site A has higher silt and clay content (4%) and total organic carbon content (0.29%) than Site B (1% and 0.06%, respectively), generating differences in macroinvertebrate abundance between sites (T. Kuwae, unpublished).

Fieldwork was performed throughout new-moon spring tidal emersion periods during the day and at night, from 27 January to 1 February 2003 and from 19 to 24 January 2004. Potential predation danger for Kentish plovers is very low at the site; no falcons were seen during the study period.

Behavioural observations

Observations of foraging action, feeding, and defecation during the day were performed using a visible-light digital camcorder (Canon, XL1S) with a telephoto zoom lens (Canon, EF 100–400 mm f/4.5–5.6L IS USM) or a mono-focal telephoto lens (Canon, EF 400 mm f/2.8L IS USM) through a lens adaptor (Canon, EF Adaptor XL). A focus length extension lens (Canon, Extender EF 1.4 \times II or \times EF 2.0 \times II) was used when needed for a high magnification. Video images with a focal length of 720–5,760 mm (20.6–164.6 \times optical magnification) were gained by this system. The recorded video images were replayed and analyzed using slow-motion and stop-motion replay modes, making it possible to detect the quick feeding actions of plovers, which usually completed within 0.2 s (see [Discussion](#)).

To investigate foraging action and defecation occurrence at night, a thermal infrared imaging system (FLIR Systems, ThermaCAM SC-3000, quantum well infrared photodetector) with a telescope lens [field of view $5^\circ \times 3.75^\circ$, focal length ca. 400 mm (11.4 \times optical magnification)] and a digital camcorder was used (Fig. 2). The occurrence of feeding could not be determined because poikilothermic prey were not sufficiently highlighted by the thermal infrared images. Instead, I used nocturnal defecation rate as a proxy for nocturnal feeding rate, assuming that feeding rate is in proportion to defecation rate.



Fig. 2 A thermal infrared video image with a dropping (*arrow*) of the Kentish plover, *Charadrius alexandrinus*. The clear contrast of the dropping is due to its higher temperature than the background

Individuals were randomly selected for video recording during the day and night observations. Repeat sampling of the same individual was avoided. Only sufficiently magnified images were used for data analyses to detect the feeding of plovers on small prey.

The foraging behaviour of Kentish plovers was classified as “pecking” (a single touch of the bill tip to the sediment surface; 98.4% of cases) or “probing” (an insertion of the bill tip into the sediment; 1.6%). I pooled pecking and probing as a total foraging attempt for analysis. FAR was calculated as the number of actions per unit foraging time. Non-foraging time, including resting, vigilance against aircraft (an airport is present near the study site), and interference competition (very scarce) was deducted to yield foraging time. The observation time for each individual was 4.1 ± 0.2 min (mean \pm SE, $n = 178$).

Environmental parameters

For the measurement of macroinvertebrate abundances, core samples were taken to a depth of 20 cm with an acrylic tube (25 cm long \times 7 cm inner diameter) at each site on the middle days of the 2003 and 2004 observation periods ($n = 4$ for each case, $n = 16$ in total). The sediment in each core was sieved (1 mm mesh), macroinvertebrates were preserved in neutralized 10% formalin-seawater solution and stored for later counting.

Light intensity was measured using a light quantum sensor (Sanyo-Sokki, MPQ-I) deployed at the site. I defined “night” as when the measured light intensity showed zero and “day” otherwise. Air temperature and wind speed were monitored hourly ca 3.0 km north of the study site by the Japan Meteorological Agency.

Using the wind speed data, wind speed at the study site was calculated according to the logarithmic law and the roughness of terrain (Davenport 1961), following confirmation of the applicability using several wind speed data at the site. The time of emersion (sediment exposure to air) for each tide was determined from the video images.

Statistical analyses

A GLM was used to examine the effect of light (day vs. night, categorical data), site (Site A vs. Site B, categorical data), temperature (continuous data), time after emersion (continuous data), and wind speed (continuous data) on FAR. Heteroscedasticity and normality of errors in various GLM structures were assessed according to Crawley (2005). The GLM with a Gaussian error distribution, an identity link function, and a log-transformed FAR as the response variable was the best model structure, and was used for the analysis. A priori selection of candidate models was based on the principle of parsimony and scientific plausibility (Burnham and Anderson 2002). The global model was fitted with all explanatory variables (light, site, temperature, time after emersion, and wind speed) and the second order interactions (Pienkowski 1983a; Piersma 1987; McNeil et al. 1992), except for continuous variables \times continuous variables.

Akaike's Information Criterion (AIC) was used to compare the fits of candidate models. Since the ratio of the sample size to number of predictor variables in the global model was less than 40, the bias-corrected AIC (AIC_C) was used (Hurvich and Tsai 1989). The best fitting model has the smallest AIC (AIC_{min}), and the difference in AIC values between models indicates the relative support for the models. Therefore, for model i , the AIC difference (Δ_i) was calculated as: AIC _{i} – AIC_{min}. Since best fitting model is often highly variable and thus has uncertainty, inference based on a single best fitting model can cause bias. To reduce model selection bias, multimodel inference was implemented using a confidence set of models (Burnham and Anderson 2002). A confidence set was selected to include only the candidate models with $\Delta_i < 4$, because models with $\Delta_i > 4$ are considerably less likely to approximate the true model (Burnham and Anderson 2002).

To interpret the relative likelihood of a model in confidence sets, an Akaike weight (w_i) was calculated according to Burnham and Anderson (2002); w_i is the probability that model i would be selected as the best fitting model in the confidence set. Selection

probability for predictor variables was calculated as summing w_i across all the models in the confidence set. Such a model averaging technique, weighted by w_i , was also used for coefficient estimates. For coefficient β_j , the model-averaged estimate $\bar{\beta}_j$ was calculated as:

$$\bar{\beta}_j = \sum_{i=1}^R w_i \hat{\beta}_{j,i}^+ \quad (1)$$

where $\hat{\beta}_{j,i}^+$ is the estimate of β_j if predictor j is included in model i , or is zero otherwise (Burnham and Anderson 2002). The standard error of $\bar{\beta}_j$ was calculated as:

$$SE(\bar{\beta}_j) = \sum_{i=1}^R w_i \sqrt{SE(\hat{\beta}_{j,i}^+)^2 + (\bar{\beta}_j - \hat{\beta}_{j,i}^+)^2} \quad (2)$$

The bias on coefficient estimates was estimated as: $SE(\bar{\beta}_j)/|\bar{\beta}_j|$. In the present study, the predictor variables that meet both the selection probability >0.9 and the bias on coefficient estimates <1.2 are considered to be strongly supported by the models.

A GLM with a logit link function was used to examine factors affecting FS. The predictor variables included in the global model were site, temperature, time after emersion, wind speed, and the second order interactions, except for continuous variables \times continuous variables. The effect of light was not examined because no data were available (prey capture was unable to be confirmed by the thermal infrared images). Since the global model was overdispersed, quasibinomial error distribution was selected for the model structure. The subsequent model selection and multimodel inference used the same procedure as for FAR, except for using QAIC_C to compare the fits of candidate models (Burnham and Anderson 2002).

Since there were censored data in defecation rate (no defecation occurrence in the video sequence for some individuals), statistical analysis using simply calculated defecation rates (number of defecation/observation time) would generate great errors and uncertainty. Thus, a survival analysis was implemented using time-to-defecation occurrence (TDO) for all defecation-observed birds, censoring time (total observation time) otherwise, and censoring parameters (binary data where defecation-observed birds, data = 1; otherwise, data = 0). If defecation occurred more than once during an observation sequence, time to first occurrence was used. Comparison of different error distributions revealed that a Weibull error distribution gave the lowest residual deviance and was selected for the model (Crawley 2005). I selected light,

temperature, time after emersion, wind speed, and the second order interactions, except for continuous variables × continuous variables, as predictor variables in the global model. The effect of site was excluded because there is a time lag between ingestion and defecation (gut throughput time), which can conceal site-specific defecation rate for plovers that may forage on both sites. The subsequent model selection and multimodel inference used the same procedure as for FAR. All statistical analyses were performed using R 2.1.1 (R Development Core Team 2005).

Results

Environmental parameters

There was no rainfall during the observation period. Temperature and wind speed ranged from −3.1 to 11.6°C and 0.0 to 7.2 m s^{−1}, respectively. Emersion period was 5.8 ± 1.2 h day^{−1} (mean ± SD, n = 10) during the day and 9.7 ± 0.9 h day^{−1} at night (mean ± SD, n = 10).

The Nereididae polychaetes (*Neanthes japonica* (Izuka) and *Ceratonereis erythraeensis* (Fauvel)) and the Ocypodidae sand-bubbler crab (*Scopimera globosa* (De Haan)) dominated the macrofauna at the site. As

far as the first prey item consumed by each Kentish plover in the video sequences were identified, only these species were taken (polychaetes 78.8%, sand-bubbler crab 21.2%). This was consistent with a previous study at the site (Yoshiyasu and Ozaki 2002). Most captured polychaetes had a stretched length of 10–40 mm and a width of less than 1 mm. The density of prey species (polychaetes + crabs) was 3.5 ± 0.7 ind core^{−1} (mean ± SE, n = 8) at Site A and 0.3 ± 0.2 ind core^{−1} (mean ± SE, n = 8) at Site B. The density of prey was not significantly different between 2003 and 2004 at either Site A (Mann–Whitney *U*test, *U*_{4,4} = 3, *P* = 0.144) and Site B (*U*_{4,4} = 4, *P* = 0.127) but was significantly higher at Site A than that at Site B for both 2003 (*U*_{4,4} = 0, *P* = 0.013) and 2004 (*U*_{4,4} = 1, *P* = 0.036).

Foraging attempt rate (FAR)

The model selection result for FAR strongly supported the effects of site, temperature, wind speed, and site × wind interaction (selection probability 1.00, bias 0.2–0.7) (Table 1). The model supported (1) a higher FAR at the high prey density site (Site A) than the low prey density site (Site B) ($\bar{\beta}$: positive, see also Fig. 3a), (2) an increased FAR with increasing temperature ($\bar{\beta}$: positive, Fig. 4a), and (3) a decreased FAR with

Table 1 Model selection results for foraging attempt rate (FAR) in Kentish plovers

	Site	Temp	Wind	TAE	Light	Site × Wind	Site × Temp	Site × Light	Site × TAE	Light × Temp	AIC _C	Δ _i	w _i
AIC best	x	x	x			x					62.79	0.00	0.21
	x	x	x	x		x					63.59	0.81	0.14
	x	x	x			x	x				64.38	1.59	0.09
	x	x	x		x	x		x			64.84	2.05	0.08
	x	x	x		x	x					64.86	2.07	0.07
	x	x	x	x		x	x				64.87	2.09	0.07
	x	x	x	x	x	x		x			64.88	2.09	0.07
	x	x	x	x		x			x		65.67	2.88	0.05
	x	x	x	x	x	x					65.69	2.90	0.05
	x	x	x	x	x	x	x	x			65.88	3.10	0.04
	x	x	x		x	x	x	x			66.15	3.36	0.04
	x	x	x	x	x	x		x		x	66.24	3.46	0.04
	x	x	x		x	x	x				66.37	3.59	0.04
Selection probability	1.00	1.00	1.00	0.47	0.43	1.00	0.29	0.27	0.05	0.04			
$\bar{\beta}$	0.610	0.019	0.021	−0.005	0.016	−0.100	0.006	−0.054	0.000	−0.001			
SE($\bar{\beta}$)	0.133	0.008	0.014	0.007	0.041	0.034	0.012	0.091	0.001	0.002			
Bias	0.2	0.4	0.7	1.5	2.7	0.3	2.1	1.7	4.0	2.4			

The predictor variable included in the selected models is shown as x

TAE time after emersion; Δ_i AIC difference calculated as AIC_i − AIC best; w_i Akaike weight showing the probability that model *i* would be selected as the best fitting model in the confidence set; $\bar{\beta}$ model-averaged coefficient estimate; $\bar{\beta}$ for categorical predictor variables (site and light) indicates a difference between two intercepts, i.e. Site A − Site B for site and night − day for light; $\bar{\beta}$ for interactions indicates a difference between two slopes, for example, slope for wind speed at Site B is 0.021 (appeared in $\bar{\beta}$ for wind) and that at Site A is −0.100 (appeared in $\bar{\beta}$ for site × wind) + 0.021; SE($\bar{\beta}$); standard error of $\bar{\beta}$; Bias bias on coefficient estimate calculated as SE($\bar{\beta}$)/| $\bar{\beta}$ |

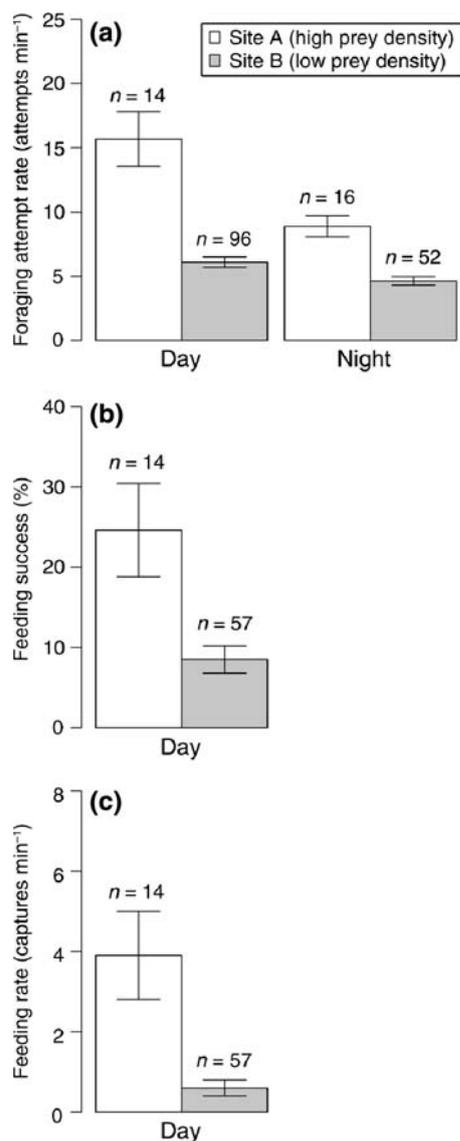


Fig. 3 **a** Diurnal and nocturnal foraging attempt rate (*FAR*), **b** diurnal feeding success (*FS*), and **c** diurnal feeding rate in Kentish plovers. *Errors bars* indicate SE

increasing wind speed at Site A (β : negative, Fig. 5a) but a slightly increased FAR with increasing wind speed at Site B (β : positive). In turn, the model poorly supported the effects of light (Fig. 3a), time after emersion (Fig. 6a), and the other interactions on FAR (selection probability 0.04–0.47, bias 1.5–4.0).

Feeding success (FS)

The model selection result for diurnal FS strongly supported the effect of site (selection probability 1.00, bias 0.3) and moderately supported the effects of time after emersion and temperature (selection probability

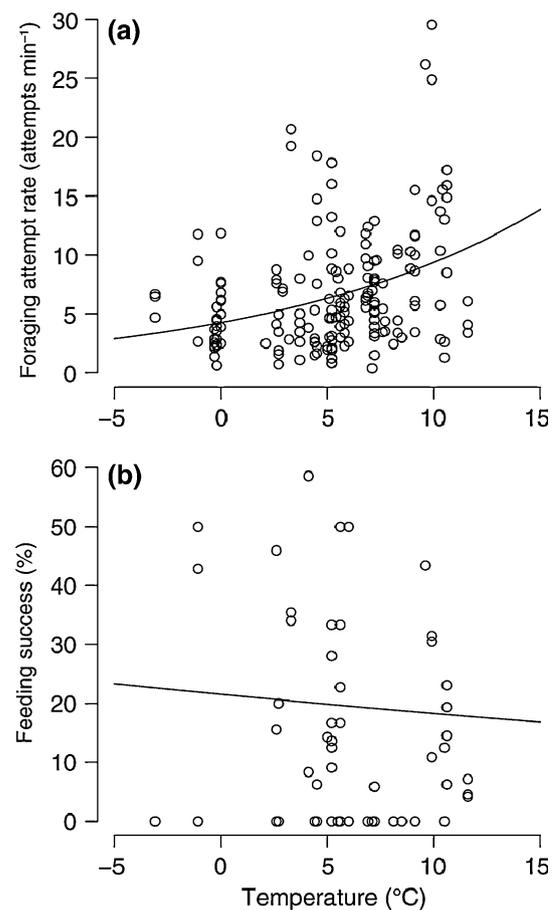


Fig. 4 Temperature versus **a** foraging attempt rate (*FAR*) and **b** diurnal feeding success (*FS*) in Kentish plovers. Note that the effects of other environmental conditions have not been removed

0.78–0.88, bias 0.5–0.6) (Table 2). The model supported (1) a higher FS at the high prey density site (Site A) than the low prey density site (Site B) (β : positive, Fig. 3b), (2) an increased FS with increasing time after emersion (β : positive, Fig. 6b), and (3) a decreased FS with increasing temperature (β : negative, Fig. 4b). In turn, the model poorly supported the effects of wind (Fig. 5b) and the other interactions on FS (selection probability 0.09–0.52, bias 1.1–2.3).

Time-to-defecation occurrence (TDO)

The model selection result for TDO strongly supported only the effect of light (selection probability 1.00, bias 1.0) (Table 3). The estimated TDO from the AIC best model was 20.8 ± 0.6 min (mean \pm SE, $n = 110$) during the day and 9.5 ± 0.4 min (mean \pm SE, $n = 68$) at night (Fig. 7). The model poorly supported the other variables (selection probability 0.11–0.59, bias 1.2–2.9).

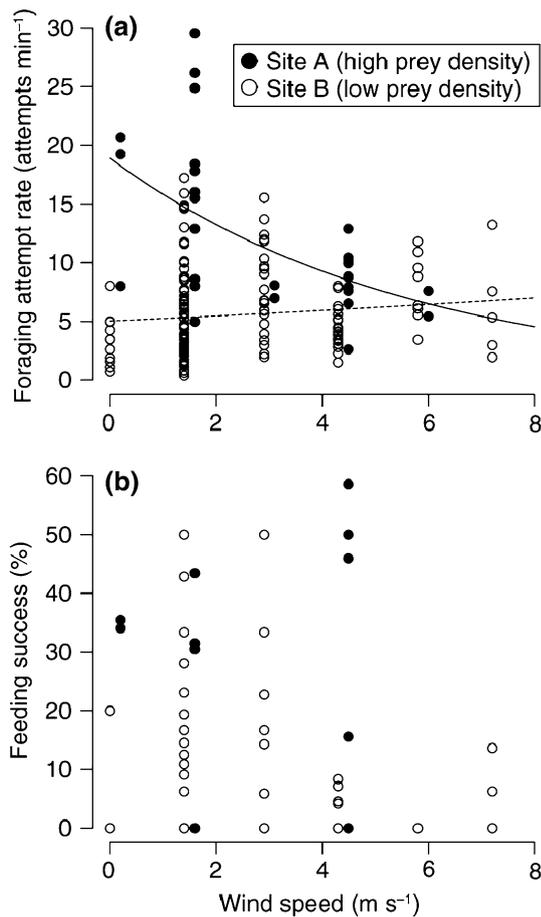


Fig. 5 Wind speed versus **a** foraging attempt rate (*FAR*) and **b** diurnal feeding success (*FS*) in Kentish plovers. Data points for Site A (*closed circle*) are offset for clarity. Note that the effects of other environmental conditions have not been removed

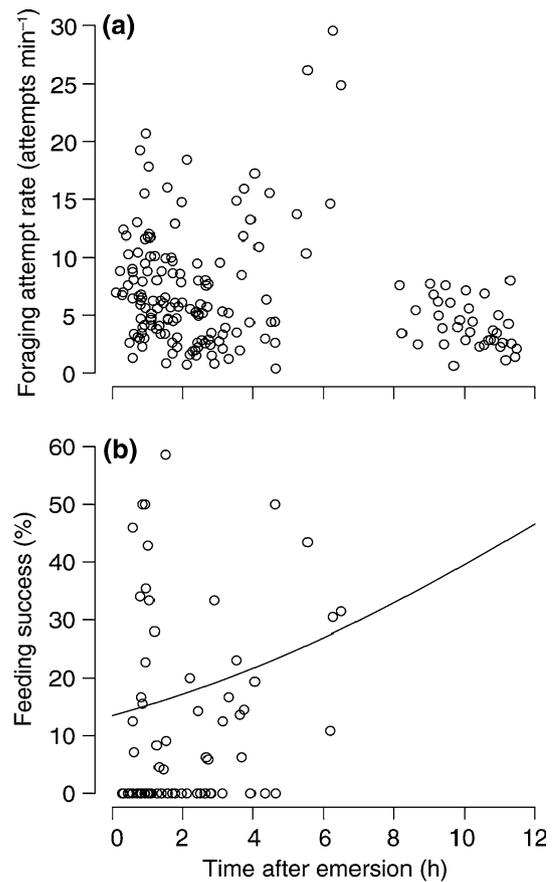


Fig. 6 Time after emersion versus **a** foraging attempt rate (*FAR*) and **b** diurnal feeding success (*FS*) in Kentish plovers. Note that the effects of other environmental conditions have not been removed

Table 2 Model selection results for feeding success (*FS*) in Kentish plovers during the day

	Site	TAE	Temp	Wind	Site × Temp	Site × TAE	Site × Wind	QAIC _C	Δ_i	w_i
AIC best	x	x	x					107.09	0.00	0.16
	x	x	x	x				107.16	0.07	0.16
	x	x	x		x			108.31	1.22	0.09
	x	x	x	x	x			108.33	1.24	0.09
	x							108.78	1.69	0.07
	x	x	x	x			x	109.12	2.03	0.06
	x	x						109.19	2.10	0.06
	x	x	x	x	x			109.36	2.27	0.05
	x			x				109.47	2.38	0.05
	x	x	x			x		109.48	2.39	0.05
	x	x	x		x	x		109.53	2.44	0.05
	x	x	x	x		x		109.60	2.51	0.05
	x	x		x				109.86	2.76	0.04
	x	x	x	x	x		x	110.42	3.33	0.03
Selection probability	1.00	0.88	0.78	0.52	0.31	0.20	0.09			
$\hat{\beta}$	1.412	0.210	-0.102	-0.072	-0.061	0.034	0.012			
SE($\hat{\beta}$)	0.393	0.104	0.059	0.076	0.092	0.078	0.024			
Bias	0.3	0.5	0.6	1.1	1.5	2.3	2.0			

Keys: see Table 1

Table 3 Model selection results for time-to-defecation occurrence (TDO) in Kentish plovers

	Light	TAE	Temp	Wind	Light × TAE	Light × Temp	AIC _C	Δ _i	w _i
AIC best	x	x			x		695.15	0.00	0.21
	x		x				695.73	0.58	0.16
	x	x					696.66	1.51	0.10
	x						697.04	1.89	0.08
	x		x			x	697.13	1.98	0.08
	x	x	x		x		697.20	2.05	0.07
	x	x		x	x		697.22	2.07	0.07
	x	x	x				697.40	2.25	0.07
	x		x	x			697.81	2.66	0.05
	x			x			698.29	3.14	0.04
	x	x		x			698.49	3.34	0.04
	x	x	x		x	x	698.97	3.82	0.03
Selection probability	1.00	0.59	0.46	0.21	0.39	0.11			
$\hat{\beta}$	-1.275	-0.069	-0.026	-0.009	0.113	-0.009			
SE($\hat{\beta}$)	1.231	0.106	0.043	0.027	0.138	0.019			
Bias	1.0	1.5	1.7	2.9	1.2	2.2			

Keys: see Table 1

Discussion

Light

Model selection results poorly supported the effect of light on FAR (Table 1). This would indicate that Kentish plovers are well-adapted to nocturnal visual searching for prey because of their large eyes and retinal visual receptors (Rojas de Azuaje et al. 1993; Thomas et al. 2006). Rojas de Azuaje et al. (1999) have examined the retinal structure and function of birds, including electroretinograms, retinal sensitivity, and rod/cone ratios, and concluded that plovers and stilts are well-adapted to nocturnal vision.

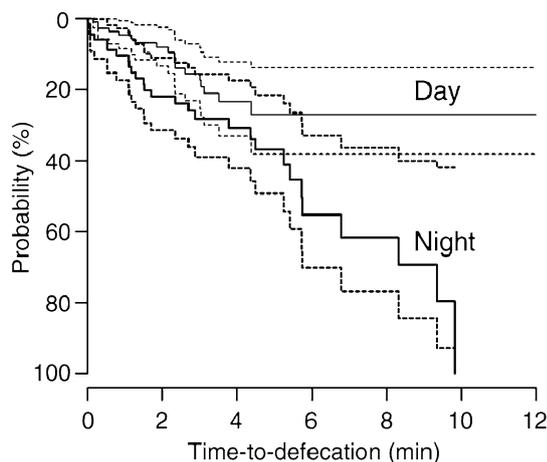


Fig. 7 Probability curves for time-to-defecation occurrence (TDO) in Kentish plovers. Solid lines and broken lines indicate averages and 95% confidential intervals, respectively

The model support for shorter TDO at night than during the day (Table 3) suggests higher feeding rate at night. Assuming that feeding rate is simply in inverse proportion to TDO (night 9.5 ± 0.4 min, day 20.8 ± 0.6 min), estimated nocturnal feeding rate is 2.2-fold higher than estimated diurnal feeding rate. In the present study period, available foraging time (emersion time) at night was 1.7-fold longer than that during the day. Hence, Kentish plovers could have captured 3.7-fold (2.2×1.7) more prey at night than during the day, i.e. nocturnal feeding could cover 79% of daily captures. Combination of this evidence and the poor model support for the effect of light on FAR suggests higher FS at night than during the day. By applying 2.2-fold higher nocturnal feeding rate, FS at night can be estimated to rise up to 54% at Site A and 19% at Site B. These estimates are comparable with those have been observed during the day in grey plovers *Pluvialis squatarola* (L.), ranging from 22 to 58% (Baker 1974; Turpie and Hockey 1993; Kuwahara 1996).

The shorter TDO at night than during the day may be explained by vigorous prey activity at night. Nereididae polychaetes, which dominated the captured prey of Kentish plovers (78.8%), are well known to be nocturnal (Last and Olive 1999, 2004), although the habits of Ocypodidae sand-bubbler crabs with respect to light are unclear (Gherardi and Russo 2001). Predominant nocturnal activity in Nereididae polychaetes can increase availability of cues at night, which may enhance an increase in FS for effective foraging by the plovers. If nocturnal activity of prey increases the frequency of cues, one can expect higher FAR at night than during the day; however, this was not the case

here. This could mean a constraint by light, i.e. an increased frequency of cues is cancelled by lower visual acuity or sensitivity at night.

To my knowledge, this is the first study showing both quantitative data for nocturnal defecation rate and an indication of a higher in situ feeding rate at night than during the day in any shorebird, although there are several reports on nocturnal feeding rates in oystercatchers *Haematopus ostralegus* (L.), whimbrels *Numenius phaeopus* (L.), and grey plovers (Goss-Custard and Durell 1987; Zwart and Dirksen 1990; Turpie and Hockey 1993), showing similar or lower intake rates at night than during the day. There are two hypotheses explaining nocturnal feeding in shorebirds: the “supplementary hypothesis” and the “preference hypothesis” (McNeil et al. 1992). The supplementary hypothesis is that, for overwintering shorebirds in temperate regions, nocturnal feeding is viewed as a compensation to meet daily energy demands, because diurnal feeding alone has been reported to be insufficient to balance energy budgets due to restriction of foraging time by short day length (e.g. Goss-Custard 1977). The preference hypothesis, in turn, states that shorebirds prefer to feed at night because it is more profitable feeding opportunity. Results from this study suggest that, promoted by increased prey availability at night, Kentish plovers use nocturnal feeding as a major activity for daily energy intake, and thus the present study supports the preference hypothesis.

Prey density

Model selection results supported the effect of site on FAR and FS (Tables 1, 2). Judging from the differences in site characteristics (see [Methods](#) and [Results](#)), the main explanatory factor may be prey density. The positive effect of high prey density on both FAR (2.2×) and FS (2.9×) resulted in a synergistic positive effect on feeding rate (6.5×) (Fig. 3c). The positive effect of prey density on FAR and FS may be resulted from an increased frequency of visual cues and the plovers’ rigorous assessment of more reliable cues for efficient foraging, respectively, as has been speculated for other shorebird species (Goss-Custard 1970, 1977; Turpie and Hockey 1993; Kalejta and Hockey 1994; Zharikov and Skilleter 2003; Lourenço et al. 2005).

Temperature

The model results supported a positive relationship between FAR and temperature but a negative relationship between FS and temperature (Tables 1, 2). The latter contrasts with my prediction that high tem-

peratures should increase the frequency of cues and have a positive effect on FS because of the plovers’ assessment of more reliable cues. Therefore, I conclude that the opposite effect of temperature on FAR and FS was caused by high temperatures stimulating both the frequency of cues and the escape ability of prey. To date, relationships between shorebirds’ feeding rate and temperature have remained unclear (see Pienkowski 1983b). However, in the present study, the breakdown of feeding rate into FAR and FS and separate investigation facilitated the uncovering of a new mechanism.

A stimulation of FAR by increasing temperatures may be attributable to the fact that polychaete activity levels are stimulated with increasing temperatures (e.g. Pienkowski 1983c; Yokoyama 1988; Deschênes et al. 2005), resulting in an increased frequency of cues. In addition, at low temperatures, polychaetes burrow deeper in the sediment (Evans 1979; Esselink and Zwarts 1989), likely resulting in a decreased frequency of cues and the subsequently reduced FAR. Thermoregulatory costs would induce the opposite effect to my result and was not the case here. A negative relationship between FS and temperature, in turn, can be explained by the escaping activity of prey, i.e. locomotion of prey into deeper sediments where shorebird bills were unable to reach. The increased speed of the locomotion at high temperatures is likely to enhance the capture failure of plovers.

Time after emersion and wind

Model selection results poorly supported the effect of time after emersion on FAR (Table 1). Time after emersion can affect prey activity through sediment desiccation. It has been reported that the polychaete *Nereis (Hediste) diversicolor* (Müller) is located in sediment surfaces when the sediments is wet following emersion; however, *N. diversicolor* migrates into deeper layers when the sediments become less wet (Dierschke et al. 1999). However, water content in the foreshore sediment of the Banzu intertidal flat has reported to show no significant variation with tidal level due to development of capillary fringes in the surface sediment during low tide (Kuwaie et al. 2003). Thus, the activity of infauna at the sediment surface may have not been affected by time after emersion, giving poor support for the effect of time after emersion on FAR.

The poor model support for the effect of time after emersion on FAR (Table 1) and a moderate model support for a positive relationship between time after emersion and FS (Table 2) would indicate a positive relationship between time after emersion and feeding

rate, which has also been observed in grey plovers feeding on thin polychaetes (Pienkowski 1983b). The mechanisms behind these relationships needs further investigation; however, one possible explanation is that as time after emersion increases, the plovers increase feeding rate and fat storage levels to prepare for the following unavailable foraging periods (during tidal immersion) by increasing FS.

Wind can disturb the surface of standing water on sediments and act as “noise”, interrupting visual cue detection (Pienkowski 1983a; Piersma 1987). Moreover, high winds force plovers to restrict their movement to balance the body against wind, for example by aligning the head with the wind direction. These processes may explain the negative effect of wind on FAR at the high prey density site (Table 1), although the slightly positive result at the low prey density site was unexpected.

Advantages of video imaging

Use of video imaging can contribute to accurate measurement of feeding behaviour due to a variety of advantages, including re-analysis capability and high magnification capability (up to 164.6× optical magnification used here). Moreover, frame-step replay has a great benefit for elucidating the very fast feeding motion of shorebirds (Rubega and Obst 1993). Indeed, the thin polychaetes captured by Kentish plovers were visible only while the polychaetes were being picked up from the sediment and swallowed, which lasted only 2–4 frames, corresponding to 0.07–0.13 s. Thus, replay of video images at normal-speed mode would likely overlook prey capture. For example, I repeated image analyses in the normal-speed mode replay using the video images taken on 30 January 2003 and compared the result with that by the frame-step replay. The comparison result showed that, of the total polychaetes detected by the frame-step replay, only $50 \pm 3\%$ (mean \pm SE, $n = 3$) of the polychaetes were detected by the normal-speed replay. This underestimation suggests that the focal observation technique, which is usually used for foraging behaviour studies, underestimates the feeding rate of small or thin prey. Therefore, this study highlights the usefulness of the telescopic video technique for researchers studying shorebirds that rapidly consume small prey items.

Furthermore, at night, the thermal infrared video imaging used here allows us to detect defecation due to higher dropping temperature making clear contrast with the background. Determination of nocturnal prey capture by small shorebirds is almost impossible, even when using a light intensifier with auxiliary lightings

(Robert and McNeil 1989). In such contexts, measurement of defecation rate using thermal infrared imaging can be a proxy for nocturnal feeding rate.

Conclusions

Telescopic video systems can record feeding behaviour of shorebirds more accurately than conventional focal observations. Foraging attempts (attempts/unit time) in Kentish plovers are higher (1) in areas of high prey abundance, (2) at higher temperatures, and (3) at lower wind speed (except where there is low prey abundance). Feeding success (captures/attempts) is higher (1) in areas of high prey abundance, (2) at lower temperatures, (3) with increasing time after emersion, and (4) at night. Most of these responses may be related to availability of visual cues to locate prey, which is largely dependent on prey activity. The proportion of nocturnal prey capture to total daily capture can be estimated to be 79%. This suggests that nocturnal feeding is an essential habit of overwintering Kentish plovers to satisfy their energetic needs.

Acknowledgments I thank E. Miyoshi for help during fieldwork, A. Kuwae and N. Oura for assistance on video image analysis, S. Harada and O. Masuko for video system information, and H. Shimura and K. Ozaki for shorebird information at the site. I also thank R. W. Elner, R. C. Ydenberg, K. J. Mathot, A. C. Pomeroy, and R. W. Butler for valuable comments. The manuscript was greatly improved by the valuable comments of three anonymous reviewers. This research was supported by grants to T.K. from the Port and Airport Research Institute Exploratory Research and the Japan Society for the Promotion of Science (JSPS) Postdoctoral Fellowships for Research Abroad (FY2004).

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