Migration orientation behaviour of the red-billed quelea Quelea quelea

Martin Dallimer and Peter J. Jones (correspondence), *Institute of Cell, Animal and Population Biology, University of Edinburgh, King's Buildings, Edinburgh, EH9 3JT, U.K. Email: peter.jones@ed.ac.uk*

Migration patterns in the red-billed quelea Quelea quelea have been the focus of intense research as the species is a major crop pest in Africa. The direction and timing of migration are believed to be controlled by the seasonal passage of rainfronts across Africa. In order to assess the validity of hypothesised migration directions in southern Africa, we tested the migration orientation behaviour of wild-caught red-billed queleas using Emlen orientation funnels. Queleas tested in Zimbabwe showed mean orientation directions to the west-north-west and east-south-east. Both directions are in agreement with current hypotheses explaining quelea migration.

There has been considerable interest in the migration patterns of the red-billed quelea *Quelea quelea* (e.g. Ward 1971, Bruggers and Elliott 1989) because it is a serious pest of grain crops throughout sub-Saharan Africa (Elliott and Lenton 1989). Knowledge of migration strategies could help to inform decisions relating to the management of queleas as a pest. In this paper we describe the migration orientation behaviour of queleas in the wild.

The migration patterns and the timing of the annual cycle of red-billed queleas are determined by seasonal changes in food availability (annual grass seeds, insects) and hence, ultimately, by the movements of local rainfronts (Ward 1971, Jones 1989a). A general model of quelea migrations in southern Africa was first proposed by Ward (1971) and described in detail by Jones (1989b). The suggestion (Ward 1971) that queleas could migrate in different directions at the start of the rains and so become separated into two sub-populations has been recently considered (Jones et al. 2000). Virtually all queleas leave the interior of southern Africa each year by late November, when the remaining dry grass seed germinates. The birds must then perform an *early rains migration* to parts of southern Africa where the rains had begun earlier and where fresh grass seed is by now available. There are two possible destinations: eastern South Africa and Mozambique or, alternatively, Angola to the west-north-west (Fig. 1). Rains in both areas begin in September–October (Ward 1971, Jones 1989b). There is no information on the relative proportions of the population that might fly in either direction. It is possible that were such a separation to persist during the first breeding attempt of the wet season, some degree of genetic isolation between the populations might be established. A migratory divide of this sort could therefore separate different populations of queleas flying either to early-rains quarters in the south-east or to the north-west. If queleas are divided into separate populations, this could have profound management implications.

Emlen funnels (Emlen and Emlen 1966) have been used to show that migrating birds use a wide range of cues to orient their migration behaviour. Most tested species have been nocturnal migrants in the northern hemisphere. Examples include the blackcap *Sylvia atricapilla* (Berthold et al. 1992) and robin *Erithacus rubecula* (Sandberg 1991) in Europe and the indigo bunting *Passerina cyanea* (Emlen et al. 1976) in North America. The technique works well with diurnal species, such as the common starling *Sturnus vulgaris* (Wiltschko and Wiltschko 1985), the meadow pipit *Anthus pratensis* (Helbig et al. 1987) and the yellow-faced honeyeater *Lichenostomus chrysops* from Australia (Munro and Wiltschko 1992). The technique has not been successful in all cases, for example the European chaffinch *Fringilla coelebs* (Muheim et al. 1999), although the orientation preferences of this species have been successfully tested in Emlen funnels (Bäckman et al. 1997).

Our primary interest in this paper was not to determine the mechanisms that queleas might use to navigate but to investigate whether premigratory birds will orient in Emlen funnels and in which direction(s), in order to test the hypothesis of a migratory divide in central southern Africa. In other passerines it tends to be birds that have undergone pre-migratory fattening which show the strongest preferred orientation directions. Lean birds can show different behaviour patterns

(Sandberg 1994, Sandberg and Moore 1996). Because queleas lay down only a small amount of fat before they migrate (Ward and Jones 1977) there is only a short window of opportunity in which to test the birds while they are fattened.

In this paper we examine the migration behaviour of the red-billed quelea in Zimbabwe just prior to the migration that is prompted by the arrival of rains. We relate the migration behaviour to the energetic condition of the birds and the hypothesised migration directions.

Methods

Data collection

Fifty-two queleas from a single non-breeding roost (Lake Manyame, Zimbabwe, 17° 49′ S, 30° 30′ E) were tested for preferences in orientation direction just prior to the onset of the rains in November 1998. From this location queleas are predicted to migrate north-west towards Angola and south-south-east towards South Africa (Fig. 1). Queleas were caught in mist nets on the evenings of 15 and 16 November 1998. Significant rainfall (62.0 mm) fell two to three days after the birds were tested. At this time queleas left the sampled roost and other nearby dry-season roosts suggesting that the tested individuals had been preparing to migrate. Each bird was kept overnight and tested for preference in orientation direction the following morning.
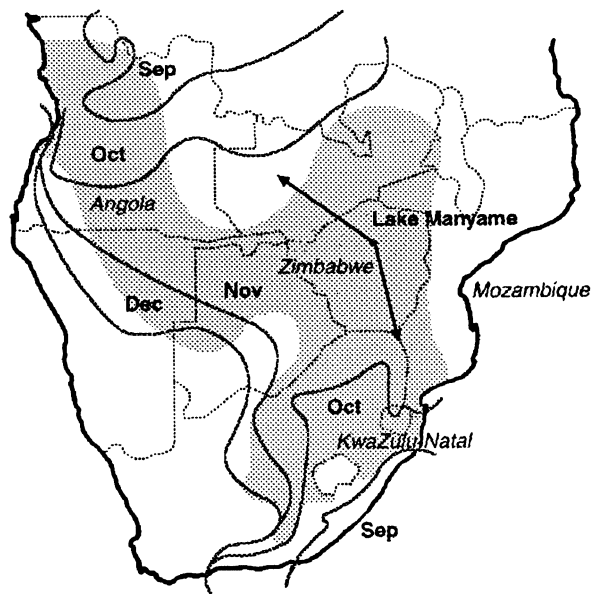

Fig. 1. Regions of early rain and predicted migration direction for red-billed queleas roosting at Lake Manyame, Zimbabwe. Contours represent the start of the wet season. The shaded region is the range of the red-billed quelea in southern Africa. Arrows indicate the predicted migration directions for queleas roosting at Lake Manyame based on Ward (1971).

In other studies with diurnal migrants (e.g. Munro and Wiltschko 1992) the time of day when the birds were most likely to migrate was known. This is not the case for queleas. It is also unknown whether queleas migrate only during the day, or if they continue at night. In the light of these uncertainties it seemed most reasonable to test queleas at the time of their peak in daily activity during the first two to three hours after dawn (Ward 1965). However, it may not be crucial to test birds during their normal migration time. When tested at sunset dunnocks *Prunella modularis* showed seasonally appropriate orientation even though they do not normally migrate at that time (Bingman and Wiltschko 1988).

Twenty queleas were tested at a time in individual Emlen funnels for 90 min. Testing started at 0530 hours and finished at 0700 hours. Sunrise was at approximately 0545 hours. Emlen funnels consisted of a funnel of aluminium with an internal height of 15 cm. At the widest point the funnel diameter was 35 cm, narrowing to 10 cm at the base. Funnels were made of a non-magnetic material to reduce the risk that it would interfere with the orientation abilities of the birds. The top of the funnel was covered with a 3 mm thick sheet of opaque Perspex which prevented the birds from seeing anything outside the funnel that may have influenced the direction in which they wished to fly, while still allowing light to enter the funnel. All tests were carried out in the shade. The position of the sun was therefore not visible to the birds. As no visual cues were available to the birds, it can be assumed that any direction preferences shown are the result of noncelestial or geomagnetic information. Each funnel was lined with a piece of typewriter correction paper (Tipp-Ex BIC, Liederbach, Germany). This recorded the scratches made by a bird's feet as it attempted to escape from the funnel. Funnels were kept upright while in use by placing them in plastic bowls. As queleas are highly sociable, funnels were kept close together.

In the case of queleas, readiness to migrate is indicated by the deposition of pre-migratory fat reserves (Ward and Jones 1977). Queleas were classified as fat (scored 1) or not fat (scored 0) depending on whether they showed any signs of fat deposition. Further discrimination of the level of fat deposition is not presented in this study due to limited sample size. Wing feathers for all individuals were fresh and not in moult. Birds had all completed their post-juvenile moult, and were about to start their pre-nuptial moult.

Data analysis

Each sheet of typewriter correction paper was subdivided into 24 sectors, and the number of scratches within each 15° sector was counted over a light table (Helbig 1991). In some sectors where scratch density

was particularly high, it was not possible to count individual scratches. Instead an estimate of the number of scratches was made by visually comparing the sector with areas of paper where the number of scratches had been accurately counted. Only birds that left at least 50 scratches on the paper were included in subsequent analyses (Emlen et al. 1976, Sandberg and Gudmundsson 1996). The mean orientation direction of individual birds was then calculated by vector addition (Batschelet 1981). Vector addition calculates a mean angle of orientation (a), which represents the direction in which the scratches on the paper are concentrated, and a mean vector length (r), which gives an indication of the degree of concentration of the scratches.

A potentially confounding issue with circular data is axiality. Axiality occurs where there is a bimodal distribution of scratches showing two modes 180° apart. In such circumstances the mean angle of orientation does not reflect either of the actual directions where scratches are concentrated and can be misleading. It is therefore important to test for axiality using the method of doubling of angles to transform a bimodal distribution into a unimodal one.

An individual was considered to have an axial distribution of scratches when the mean vector length of the scratch distribution with doubled angles was larger than that without doubled angles (Batschelet 1981). If an individual showed an axial distribution, then there are two parts to the mean vector. Only the part of the mean vector closest to that of the unimodal distribution of the same individual was used in further analysis (Muheim et al. 1999). Directionality in the distribution of scratches for each individual was tested for significance at the 0.05 and 0.01 levels using the Rayleigh test (Batschelet 1981). Significance was corrected for multiple tests using the sequential Bonferroni procedure (Rice 1989). In addition, the mean orientation direction for the population as a whole was assessed.

In order to assess the influence of fat deposition (1 – fat, 0 – lean) on either preferred direction (mean angle, a) or degree of directionality in the migrating birds (mean vector length, r), two different types of tests were used depending on whether the variable was linear or circular. The vector addition process calculates a mean angle and a mean vector. The mean angle is a circular measure and is unsuitable for use with linear statistics. Hence a pairwise Watson-Williams test was used (Batschelet 1981). However, the mean vector varies from 0 to 1, and it is appropriate to use linear statistics.

Individual mean vector length decreases with increasing number of scratches (Batschelet 1981). Mean vector length cannot therefore be used as a direct measure of concentration of scratches. Instead, the residuals from the regression equation of mean vector length on the logarithm of the number of scratches were used (y = 0.425 − 0.047x, n = 48, r = 0.5, P = 0.068) (Muheim et al. 1999). Tests for influence on the strength of prefer-ence (the mean vector length) were carried out using the residuals from the regression equation. A two-sample t-test was used to investigate the effect of fat score on the residuals of the mean vector length.

Results

Of the 52 queleas tested, 48 left more than 50 scratches indicating that they had been sufficiently active in the funnels to be used in further analysis. Thirty-seven birds had a significant directional preference and ten of these showed a significant axial distribution of scratches (Table 1). For individuals showing axial distribution, only the mean vector closest to its unimodal distribution was used in further analysis. Fig. 2 shows the population-wide distribution of individual mean angles of orientation. The population distribution shows a significant axial distribution, with the mean angle, a = 117°–297° and the mean vector, r = 0.296 (Rayleigh test, P = 0.029). The results of the paired Watson-Williams test showed that there was no significant relationship between mean angle and fat score (F = 2.92, n = 22, 26, ns). Equally, the t-test showed no significant relationships between mean vector length and fat score ($t_{42} = 0.56$, ns).

Discussion

The red-billed quelea is capable of expressing a preferred migration direction when captured and tested in Emlen funnels in the wild. Queleas in Zimbabwe showed significant directional preference towards west-north-west and east-south-east. When compared with the direction of approach of the rainfronts, the directions that queleas chose to migrate were remarkably close to those predicted (Fig. 1). The queleas tested at Lake Manyame were from a non-breeding roost at the end of the dry season as the rains were beginning. Heavy rain fell in the area shortly after the birds were tested and queleas subsequently left the area completely. Hence, the directions that queleas expressed in the Emlen funnels were very likely to have been the directions that they would initially have chosen for migration over the incoming rainfronts and away from an area where food was shortly to become scarce.

Previous orientation studies have found that it is mainly birds that have laid down fat reserves in preparation for migration that show a significant preference in orientation funnels consistent with the direction of migration (Sandberg 1994, Sandberg and Gudmundsson 1996, Sandberg and Moore 1996, Sandberg et al. 1998). Queleas do deposit fat in preparation for migration, and the mean amount of fat deposited is proportional to the distance they then travel (Ward and

Table 1. Number of scratches (N), mean direction (a), and mean vector length (r) for each red-billed quelea tested in an Emlen funnel. Distribution refers to whether the scratches were distributed unimodally or axially. The distribution of scratches was tested for significant directionality using a Rayleigh test. P-values are given after Bonferroni correction for multiple tests.

| Sample	Fat	N	Distribution	a	r	P	Sample	Fat	N	Distribution	a	r	P
LM01	lean	200	unimodal	241	0.448	<0.01	LM28	fat	81	unimodal	282	0.176	n.s.
LM02	lean	97	unimodal	200	0.338	<0.01	LM29	lean	170	axial	25–205	0.442	<0.01
LM03	lean	159	unimodal	133	0.580	<0.01	LM30	fat	73	unimodal	297	0.295	n.s.
LM04	lean	345	unimodal	239	0.273	<0.01	LM31	lean	66	unimodal	146	0.179	n.s.
LM05	lean	271	unimodal	157	0.221	<0.01	LM32	fat	89	unimodal	107	0.156	n.s.
LM06	lean	322	axial	116–296	0.268	<0.01	LM33	fat	320	unimodal	5	0.302	<0.01
LM07	lean	121	unimodal	297	0.205	n.s.	LM34	fat	305	unimodal	89	0.191	<0.01
LM09	lean	290	axial	5–185	0.282	<0.01	LM35	fat	196	axial	137–317	0.112	n.s.
LM10	lean	586	axial	155–335	0.150	<0.01	LM36	fat	60	unimodal	49	0.428	<0.01
LM11	lean	188	unimodal	348	0.325	<0.01	LM37	lean	134	unimodal	200	0.147	n.s.
LM12	lean	196	unimodal	289	0.372	<0.01	LM38	fat	38	N<50			
LM13	lean	207	unimodal	91	0.558	<0.01	LM39	fat	188	unimodal	288	0.431	<0.01
LM14	lean	120	unimodal	235	0.514	<0.01	LM40	lean	49	N<50			
LM15	lean	181	unimodal	149	0.323	<0.01	LM41	fat	258	unimodal	322	0.415	<0.01
LM16	lean	310	unimodal	302	0.278	<0.01	LM42	fat	223	unimodal	95	0.018	n.s.
LM17	lean	129	axial	2–182	0.497	<0.01	LM43	fat	397	unimodal	312	0.200	<0.01
LM18	lean	148	unimodal	15	0.220	<0.05	LM44	fat	268	unimodal	327	0.475	<0.01
LM19	lean	35	N<50				LM45	fat	222	axial	112–292	0.377	<0.01
LM20	lean	309	unimodal	142	0.253	<0.01	LM46	fat	146	unimodal	161	0.175	n.s.
LM21	lean	222	unimodal	234	0.521	<0.01	LM47	fat	155	axial	65–245	0.279	<0.01
LM22	lean	155	unimodal	107	0.091	n.s.	LM48	fat	98	unimodal	154	0.620	<0.01
LM23	lean	140	unimodal	254	0.323	<0.01	LM49	fat	27	N<50			
LM24	lean	142	unimodal	292	0.223	<0.05	LM50	lean	107	axial	105–285	0.508	<0.01
LM25	fat	248	axial	110–290	0.138	n.s.	LM51	fat	109	axial	101–281	0.444	<0.01
LM26	fat	76	axial	236–56	0.346	<0.01	LM52	fat	141	unimodal	111	0.292	<0.01
LM27	fat	139	unimodal	64	0.682	<0.01	LM53	fat	183	unimodal	312	0.236	<0.01
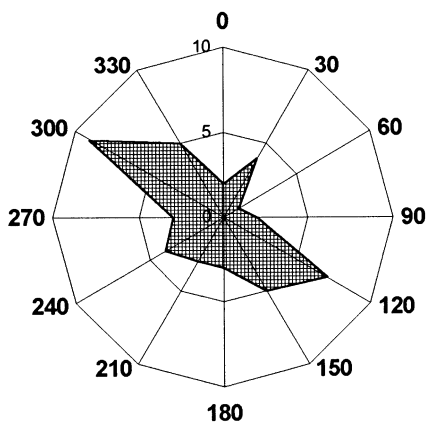
Fig. 2. Mean orientation direction of 48 red-billed queleas at Lake Manyame, Zimbabwe, showing significant axial distribution. The radial axis (from the centre to the outer circle) gives the number of birds orienting in each direction. The circular axis gives the direction in degrees: North is 0°. Axial distribution: 117°–297°, Mean vector, r = 0.296. Rayleigh test, P = 0.029.

Jones 1977). However, we found no relationship between whether individual birds had fat reserves or not and either the direction of migration or the strength with which that direction was expressed. This result is consistent with an earlier study in which all queleas in a dry season roost left together as a flock on early-rains migration, regardless of differences in energetic status between individual birds (Ward and Jones 1977). This perhaps indicates the importance of flock membership to queleas over any individual energetic demands.

Many migrant species have to cross areas of inhospitable habitat. At such ecological barriers, some tested individuals orient in the opposite direction from the route to their destination (e.g. European robin, Sandberg 1994) which can lead to a population-wide axial distribution of preferred migratory directions. The explanation proposed is that some individuals may not be in the correct physiological condition to cross the ecological barrier in question. Lean individuals backtrack to find a suitable area to regain condition before resuming migration. We found no difference between fat and lean queleas in the strength and direction of orientation. In this case the explanation for the axial distribution of direction preferences is unlikely to depend on the fuel reserves of the individuals involved.

If the behaviour of queleas in orientation funnels is not mediated by energetic considerations, it is likely that the two opposite directions in which they chose to orient at the onset of the rains were the expression of their actual migration behaviour. Some birds flew towards the rainfront arriving from the north-west and others flew towards the other rainfront arriving from the south-east, corresponding to the hypothesised early-rains migration directions in southern Africa and lending some support to the possibility of a migratory

divide in this species (Jones et al. 2000). This support must be tempered by the fact that birds just tested in funnels can show orientation preferences that are not carried out following release (e.g. Sandberg and Moore 1996, Sandberg et al. 2000). Indeed under certain conditions a bimodal pattern can be observed in funnels where no bimodality in migration directions is observed in the wild (e.g. Able and Able 1995).

Although we have found evidence that two migration direction preferences occur in the same population of queleas, it remains unknown whether individual birds show a fixed or variable response to the changing environmental conditions. Individual queleas may have a plastic, opportunistic response in migratory direction to the approach of rain and potential food shortage or, alternatively, within a single roost there are flocks following fixed, separate migration pathways.

Despite the results presented in this paper in support of a migratory divide, there is no evidence that there is any population differentiation among red-billed queleas in southern Africa (Dallimer 2000). Recent range expansion in South Africa (Whittington-Jones 1998) may be an example of queleas rapidly altering their migratory habits in response to changing environmental conditions. Such flexibility does not allow population division to develop; instead migratory birds could simply react to ecological conditions and change their migratory behaviour accordingly. One example of this phenomenon is in the south-western United States, where yellow-rumped warblers *Dendroica coronata* showed facultative migration that depended on the food resource abundance in their desert riparian habitats (Terrill and Ohmart 1984). A facultative pattern could exist whereby queleas take local environmental conditions into account before migrating along either of the possible routes.

References

Able, K. P. and Able, M. A. 1995. Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird. – J. Comp. Physiol. A. 177: 351–356.

Bäckman, J., Pettersson, J. and Sandberg, R. 1997. The influence of fat stores on magnetic orientation in day-migrating chaffinch, *Fringilla coelebs*. – Ethology 103: 247–256.

Batschelet, E. 1981. Circular Statistics in Biology. – Academic Press, London.

Berthold, P., Helbig, A. J., Mohr, G. and Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. – Nature 360: 668–669.

Bingman, V. L. and Wiltschko, W. 1988. Orientation of dunnocks (*Prunella modularis*) at sunset. – Ethology 77: 1–9.

Bruggers, R. L. and Elliott, C. C. H. (eds) 1989. *Quelea quelea* Africa's Bird Pest. – Oxford University Press, Oxford.

Dallimer, M. 2000. Migration Patterns of the Redbilled Quelea *Quelea quelea* in Southern Africa: Genetics, Morphology and Behaviour – PhD thesis, University of Edinburgh.

Elliott, C. C. H. and Lenton, G. M. 1989. Monitoring the quelea. – In: Bruggers, R. L. and Elliott, C. C. H. (eds). *Quelea quelea*: Africa's Bird Pest. Oxford University Press, Oxford, pp. 35–49.

Emlen, S. T. and Emlen, J. T. 1966. A technique for recording migratory orientation of captive birds. – Auk 83: 361–367.

Emlen, S. T., Wiltschko, W., Demong, N. J., Wiltschko, R. and Bergman, S. 1976. Magnetic direction finding: evidence for its use in migratory indigo buntings. – Science 193: 505–507.

Helbig, A. J. 1991. Experimental and analytical techniques used in bird orientation research. – In: Berthold, P. (ed.). Orientation in Birds. Birkhäuser-Verlag, Basel, pp. 270–306.

Helbig, A. J., Orth, G., Laske, V. and Wiltschko, W. 1987. Migratory orientation and activity of the meadow pipit (*Anthus pratensis*): a comparative observational and experimental field study. – Behaviour 103: 276–293.

Jones, P. J. 1989b. Distribution, populations, and migration patterns of quelea in southern Africa. – In: Bruggers, R. L. and Elliott, C. C. H. (eds). *Quelea quelea*: Africa's Bird Pest. Oxford University Press, Oxford, pp. 132–143.

Jones, P. J. 1989a. General aspects of quelea migrations. – In: Bruggers, R. L. and Elliott, C. C. H. (eds). *Quelea quelea*: Africa's Bird Pest. Oxford University Press, Oxford, pp. 102–112.

Jones, P. J., Cheke, R. A., Mundy, P. J., Dallimer, M. and Venn, J. F. 2000. *Quelea* populations and forecasting in southern Africa. – In: Cheke, R. A., Rosenberg, L. J. and Kieser, M. E. (eds). Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Institute, Pretoria, South Africa, 24–26 March 1999. Natural Resources Institute, Chatham, U.K., pp. 139–149.

Muheim, R., Jenni, L. and Weindler, P. 1999. The orientation behaviour of chaffinches, *Fringilla coelebs*, caught during active migratory flight in relation to the sun. – Ethology 105: 97–110.

Munro, U. and Wiltschko, W. 1992. Orientation studies on yellow-faced honeyeaters *Lichenostomus chrysops* (Meliphagidae) during autumn migration. – Emu 92: 181–184.

Rice, W. R. 1989. Analyzing tables of statistical tests. – Evolution 43: 223–225.

Sandberg, R. 1991. Sunset orientation of robins, *Erithacus rubecula*, with different fields of sky vision. – Behav. Ecol. Sociobiol. 28: 77–83.

Sandberg, R. 1994. Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. – Anim. Behav. 47: 679–686.

Sandberg, R., Bäckman, J. and Ottosson, U. 1998. Orientation of snow buntings (*Plectrophenax nivalis*) close to the magnetic north pole. – J. Exp. Biol. 201: 1859–1870.

Sandberg, R. and Gudmundsson, G. A. 1996. Orientation cage experiments with Dunlins during autumn migration in Iceland. – J. Avian Biol. 27: 183–188.

Sandberg, R. and Moore, F. R. 1996. Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. – Behav. Ecol. Sociobiol. 39: 1–10.

Sandberg, R., Bäckman, J., Moore, F. R. and Lõhmus, M. 2000. Magnetic information calibrates celestial cues during migration. – Anim. Behav. 60: 453–462.

Terrill, S. B. and Ohmart, R. D. 1984. Facultative extension of fall migration by yellow-rumped warblers (*Dendroica coronata*). – Auk 101: 427–438.

Ward, P. 1965. Feeding ecology of the black-faced dioch *Quelea quelea* in Nigeria. – Ibis 107: 173–214.

Ward, P. 1971. The migration patterns of *Quelea quelea* in Africa. – Ibis 113: 275–297.

Ward, P. and Jones, P. J. 1977. Pre-migratory fattening in three races of the Red-billed quelea *Quelea quelea* (Aves: Ploceidae), an intra-tropical migrant. – J. Zool. Lond. 181: 43–56.

Whittington-Jones, C. A. 1998. Apparent range expansion of the Redbilled Quelea *Quelea quelea* in the Eastern Cape Province of South Africa. – Ostrich 68: 97–103.

Wiltschko, W. and Wiltschko, R. 1985. The interactions of different orientation cues. – In: Ilyrov, V. D. and Gavrilov, V. M. (eds). Acta 18 Congr. Int. Ornithol. NAUKA, Moscow, pp. 304–331.

Swim speed of free-ranging Adélie penguins Pygoscelis adeliae *and its relation to the maximum depth of dives*

Y. Ropert-Coudert (correspondence), A. Kato, K. Sato and Y. Naito, National Institute of Polar Research, 1-9-10 Kaga, Itabashi-ku, Tokyo 173-8515, Japan. E-mail: yan@nipr.ac.jp
J. Baudat, C. A. Bost and Y. Le Maho, Centre d'Ecologie et de Physiologie Energétiques, 23 rue Becquerel, F-67087 Strasbourg cedex 2, France