Can whisker spot patterns be used to identify individual polar bears?

C. J. R. Anderson, J. D. Roth & J. M. Waterman

Department of Biology, University of Central Florida, Orlando, FL, USA

Keywords
Ursus maritimus; noninvasive; natural marking; photograph; reliability; information theory.

Correspondence
Jane M. Waterman, Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816, USA.
Email: waterman@mail.ucf.edu

Received 22 December 2006; accepted 23 March 2007

doi:10.1111/j.1469-7998.2007.00340.x

Abstract

Studies of population dynamics, movement patterns and animal behavior usually require identification of individuals. We evaluated the reliability of using whisker spot patterns to noninvasively identify individual polar bears *Ursus maritimus*. We obtained the locations of polar bear whisker spots from photographs taken in western Hudson Bay, tested the independence of spot locations, estimated the complexity of each spot pattern in terms of information and determined whether each whisker spot pattern was reliable from its information content. Of the 50 whisker spot patterns analyzed, 98% contained enough information to be reliable, and this result varied little among observers. Photographs taken <50 m from polar bears were most useful. Our results suggest that individual identification of polar bears in the field based on whisker spot pattern variations is reliable. Researchers studying polar bear behavior or estimating population parameters can benefit from this method if proximity to the bears is feasible.

Introduction

Identification of individual animals in the field is often necessary for studies involving population dynamics, movement patterns and animal behavior (Nietfeld, Barret & Silvy, 1994). For example, estimates of population size, survival and reproduction rates and immigration and emigration rates using capture–recapture models involve identifying previously marked or sighted individual animals (Nichols, 1992). Research in behavioral ecology also depends on recognition of individuals because animals differ greatly in their individual behavior, and identifying this variability aids our understanding of the evolution of these behaviors (Martin & Kraemer, 1987; Hayes & Jenkins, 1997).

Methods for identifying individual animals can be categorized as (1) invasive or (2) noninvasive. Invasive methods rely on artificial markings, such as ear tags, neck collars, transponders, tattoos, tissue removal, dyes and chemical or radioactive markers (Nietfeld *et al*., 1994). These methods are very reliable as they afford unambiguous identification (Pennycuick, 1978), and are quite useful in studies where animals are routinely handled for physical measurements (e.g. mass or blood samples) or when noninvasive identification is unfeasible. However, applying such markers possibly could affect the behavior of handled animals (e.g. Rodda *et al*., 1988; but see Borges-Landaez & Shine, 2003), and if the study does not otherwise require capture and restraint, the difficulty and expense of such methods may be prohibitive.

Noninvasive methods of identification rely on natural markings, such as facial and body scars or coloration (e.g. Pennycuick & Rudnai, 1970; Jarman *et al*., 1989; Miththapala *et al*., 1989; Bretagnolle, Thibault & Dominici, 1994; Gowans & Whitehead, 2001; Kelly, 2001; Eitam & Blaustein, 2002), and thus minimize most drawbacks of invasive methods. However, they cannot guarantee that all individuals in a population will possess unique markings (Pennycuick, 1978), and are not feasible when natural markings are difficult to see or are lacking altogether. Nonetheless, noninvasive identification is a practical alternative to invasive methods, and has been used in estimating several population parameters (e.g. Hammond, Mizroch & Donovan, 1990; Karanth & Nichols, 1998; Langtimm *et al*., 2004) and in studying animal behavior (e.g. Grinnell, Packer & Pusey, 1995; Mougeot, Thibaul & Bretagnolle, 2002).

In this study, we examined whether whisker spot patterns could be used to identify individual polar bears *Ursus maritimus* as part of a long-term study of polar bear behavior in western Hudson Bay (Eckhardt, Waterman & Roth, 2002; Eckhardt, 2005). Previous studies of polar bear behavior have used invasive identification methods (e.g. Latour, 1981*b*) or facial scars and body shape or size to identify individuals (e.g. Eckhardt *et al*., 2002; Dyck & Baydack, 2004). However, logistical constraints prohibited us from immobilizing and capturing free-ranging bears, and scars are not always present on bears and body shape or size may not be reliable. Field observations and photographs (J. M. Waterman and J. D. Roth, unpubl. data) suggest that patterns of whisker spots (small, dark, circular areas around whisker follicles distinctively arranged on each side of the anterior end of the muzzle) of polar bears may be sufficiently distinctive to use for noninvasive identification of individuals, as has been found for other large-bodied mammals (Pennycuick, 1978).

A method of identifying individuals based on whisker spot patterns was first developed for lions *Panthera leo* (Pennycuick & Rudnai, 1970). This study assessed the reliability of the method by measuring the information (i.e. complexity) contained in each pattern. Conceptually, the lower the probability that a pattern occurs in a population, the more information it contains and, thus, the more reliable it is. This information theoretic approach of assessing identification reliability was later generalized for use in other species (Pennycuick, 1978), and has been applied to whisker spot patterns on leopards *Panthera pardus kotiya* (Miththapala *et al*., 1989) and to several traits on two macropod species (Jarman *et al*., 1989). However, the utility of an identification method depends on the proportion of the population with reliable patterns. Reliable whisker spot patterns were found in 92% of lions examined (Pennycuick & Rudnai, 1970), and although using additional characters (e.g. sex, scar patterns) would improve the reliability of identification (Pennycuick, 1978), there has been little discussion in the literature about the frequency of reliable patterns needed for this method to be used with confidence. In this study, we formulated a criterion for determining the utility of an identification method. Using information-theoretic techniques (Pennycuick & Rudnai, 1970; Pennycuick, 1978), we show that polar bear whisker spot patterns can be used to reliably identify individuals, and thus could be used to develop a noninvasive identification system based on whisker spot patterns for use in studies of behavior and population parameter estimates.

Methods

Study site and photograph collection

We photographed polar bears about 30 km east of the town of Churchill, Manitoba, Canada (58° 45′N, 93° 45′W). The Hudson Bay sea-ice melts in August, forcing polar bears to aggregate along the coast until freeze-up in mid-November (Latour, 1981*b*). Access to this site was facilitated by a tundra vehicle (a large bus adapted to travel on tundra), normally used for polar bear viewing by ecotourists (Dyck & Baydack, 2004). No more than 18 tundra vehicles were permitted in this 8 km^2 area, and polar bears rarely responded to the approach of these vehicles (Eckhardt, 2005) and were free to leave the area at any time.

Photographs were taken daily (09:00–15:00 h) by trained volunteers and the authors during October 18–November 11, 2003, October 18–November 10, 2004 and October 18–November 10, 2005. We used Nikon D100 6.0-megapixel digital cameras equipped with 70–300 and 80–400 mm lenses (Nikon, Melville, NY, USA) to photograph bears. Polar bears were individually identified by distinct facial scars, sex and body shape and size. We took several photographs of the same bear at different angles as the bear moved, especially as facial profiles came to view. We used a laser range-finder (Bushnell Yardage Pro 1000, Bushnell, Overland, KS, USA) to measure the distance to bears for some photographs.

Whisker spot selection

For our analyses, we selected the best 50 polar bears based on their photographic quality (determined by focus, clarity and resolution) and angle (determined by the extent a bear's facial profile was perpendicular to the camera's axis). Photographs were enhanced with Adobe Photoshop 7.0 to improve brightness and contrast, and were rotated and/or flipped so that the front corner of the eye and the notch of the nose were aligned horizontally with the nose pointing to the right, creating the abscissa for a relative coordinate system where the eye was at the origin and the nose at 1.0 (Fig. 1).

Whisker spot locations were marked on the highest quality and best angle image for each bear; additional photographs of the same bear were sometimes available to confirm spots locations. Polar bear whisker spots are found each side of the bear's anterior end of the muzzle, between the nose and the upper lip, roughly aligned into three to four rows. Dark bands and spots that blend with the black upper lip were not considered whisker spots. To reduce statistical bias caused by possible correlation between whisker spot patterns on each side of a bear, only one side was used in our analyses. The relative location of each whisker spot was determined by dividing the x and y coordinates (in pixels) by the distance between the eye and the nose (in pixels).

Information content and reliability of spot patterns

A pattern must be divided into mutually independent characters, each taking at least two values, before its information content can be calculated (Pennycuick, 1978). By fitting a regular grid on the relative coordinate system described earlier, every spot pattern was divided into characters, with each character having a value of either 'present' or 'absent.' The size of each grid cell was 0.05×0.05 (relative units), a conservative size determined by the maximum distance found between the same whisker spots on two different photographs of the same bear. Character A1, for example, denotes whether at least one spot is present within the cell defined by $0 \leq x < 0.05$ and $0 \leq y < 0.05$ (Fig. 1). Similarly, character B2 denotes whether at least one spot is present within $0.05 \leq x < 0.1$ and $0.05 \leq y < 0.1$, and so on (spots with $x > 0.95$ were not used in our analyses because whisker spots present on that region were difficult to distinguish).

As discussed by Pennycuick & Rudnai (1970), if a whisker spot is present in character i in n_i patterns, the frequency of occurrence f_i of a spot for that character is defined as

$$f_i = \frac{n_i}{N}$$

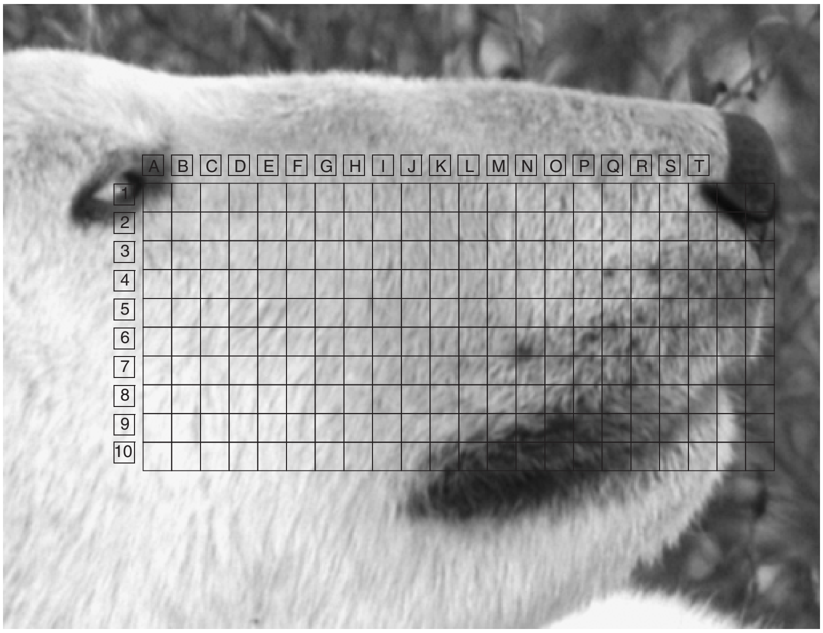

Figure 1 Grid superimposed on polar bear *Ursus maritimus* photograph. The grid divides a spot pattern into characters, with each character having a value of either 'present' or 'absent,' depending on whether a spot occurs in the corresponding cell.

where N is the number of patterns (i.e. polar bears) in the sample. Assuming that the characters in a whisker spot pattern are mutually independent (an assumption we examine later), the probability of occurrence of the spot pattern in the study population is

$$P = f_a \times f_b \times f_c \times \cdots \times (1 - f_q) \times (1 - f_r) \times (1 - f_s) \times \cdots$$

where characters a, b, c, etc. of the pattern have spots, and characters q, r, s, etc. do not (Pennycuick & Rudnai, 1970). For each whisker spot pattern in the sample, the value of P was calculated and expressed in terms of its information content $I = -\log_2 P$ (Pennycuick & Rudnai, 1970).

Identification is considered 'reliable' if the probability that two or more indistinguishable individuals exist in the study population is less than some arbitrary value ε (Pennycuick & Rudnai, 1970). Thus, the probability that at most one individual in the population has a particular pattern must be $> 1 - \varepsilon$ (Pennycuick & Rudnai, 1970). This relationship can be expressed as

$$(1 - P)^M + MP(1 - P)^{M-1} > 1 - \varepsilon$$

which represents the probability that at most one individual in a population of M individuals has a pattern with probability P (Pennycuick & Rudnai, 1970).

For a polar bear whisker spot pattern to be reliable, we required that its probability of duplication in our western Hudson Bay population of 1000 polar bears (Regehr *et al.*, 2005) be $< 1\%$ ($\varepsilon = 0.01$). Using the above equation, the maximum value of P was estimated to be 1.4862×10^{-4} or, in terms of information, 12.72 bits. Hence, for an individual bear to be reliably identified in our study population, its whisker spot pattern must contain > 12.72 bits of information.

Mutual independence of spots

Calculation of the probability of occurrence of a spot pattern in a study population requires that all characters of the pattern be mutually independent (Pennycuick, 1978). A set of events $E = \{E_1, E_2, \ldots, E_n\}$ is mutually independent if for every subset of the events, their joint probability is equal to the product of their individual probabilities (Larson, 1982). In other words, $P(E_i \cap E_j) = P(E_i)P(E_j)$ must hold for all distinct i and j; $P(E_i \cap E_j \cap E_k) = P(E_i)P(E_j)P(E_k)$ must hold for all distinct i, j and k; and so on until $P(E_1 \cap E_2 \cap \ldots \cap E_n) = P(E_1)P(E_2)\ldots P(E_n)$. To determine whether all characters of a spot pattern were mutually independent, we defined E_i as the event in which character i had the value 'present.' Because there were not enough spot patterns to satisfy all combinations of spot occurrences required for a test of mutual independence, we only tested whether characters were pairwise independent, which is always satisfied when characters are mutually independent.

Therefore, we tested whether the joint probability of characters i and j having a value of 'present' was equal to the individual probability of character i having a value of 'present' multiplied by the individual probability of character j having a value of 'present.' We called the joint probability 'observed' because it was determined from the observed proportion of spot patterns that contained spots at locations i and j, and we called the product of the two individual probabilities 'expected' because it was determined from the spot probability distribution (Fig. 2). In addition, because each character could also have the value of 'absent,' we tested for the events in which one or both characters in each pairwise comparison had the value of 'absent.'

	J	K	L	M	N	O	P	Q	R	S
2			0.02							
3								0.04	0.08	0.10
4					0.02		0.04	0.20	0.26	0.66
5				0.02	0.02	0.02	0.04	0.14	0.36	0.58
6				0.04	0.04	0.04	0.12	0.24	0.48	0.66
7				0.06	0.22	0.46	0.50	0.52	0.54	0.38
8	0.02				0.18	0.24	0.22	0.16	0.28	0.08
9						0.02		0.04		

Figure 2 Characters (represented as grid cells) from all 50 spot patterns analyzed. Each cell contains the probability of its corresponding character having a value of 'present.'

To test for significant differences between the observed and expected probabilities, we performed randomization tests (Quinn & Keough, 2002) for each possible pair of characters. We randomly generated 5000 samples of 50 spot patterns such that each sample retained the probability distribution determined from our original sample of bears (Fig. 2). For each pair of characters in the randomized samples, we calculated their observed probabilities and determined the proportion that deviated from their expected probability at least as much as did the nonrandomized sample. If this proportion was <0.01 (see Quinn & Keough, 2002), the true deviation between the observed and expected probabilities for that particular pair of characters was too great to be explained by chance, and so those characters were nonindependent. Therefore, we eliminated the character that, on average, contributed the least amount of information to a pattern, and thus preserving the more useful character.

Utility of identification method

Our *a priori* criterion for confidence in using this identification method was that $>95\%$ of whisker spot patterns in our sample must be reliable (i.e. their information content was >12.72 bits). To account for sample error, we calculated the proportion of reliable patterns from 10 000 whisker spot patterns randomly generated from our sample spot probability distribution (Fig. 2).

Consistency of analyses

The best image selected for each polar bear and the whisker spots marked on each image were chosen by a single judge (one of the authors). To test whether our analyses were contingent upon the observer who selected the images and marked the whisker spots, two additional judges (the other two authors) were provided the same images that the first judge used. Like the first judge, they selected the image they thought had the highest quality and angle for each polar bear, and marked the locations of the eye, nose and whisker spots on those images. Judges were allowed to use additional images for the same bear (if available) that the first judge used for confirmation of spot locations. For each set of whisker spot patterns, the same analyses were performed: a character set was derived and nonindependent characters were removed, the information content of each pattern was calculated for the sample and randomized patterns and the proportions of those that were reliable were determined.

Results

We took over 10 000 polar bear photographs for all years combined, of which about 10% were appropriate for identification (i.e. the polar bear's face was clearly visible). Over 200 individual polar bears were identified based on facial scars, sex and body shape and size. From the 50 polar bears selected for this study, we chose 167 photographs of relatively high quality to use to identify whisker spots.

We found a total of 39 characters from our sample of whisker spot patterns (Fig. 2). Characters S6 and S4 had the highest probability of spot occurrence, 0.66, which indicated that 66% of polar bears had at least one spot within those cells. Thus, the presence of a spot within cells S6 or S4 adds only 0.60 bits of information to a pattern. Conversely, characters with spot occurrence probabilities of 0.02 indicated that only one polar bear had a spot within those cells, whose presence adds 5.64 bits of information to a pattern. The amount of information that other characters add to a pattern if a spot is present there can be calculated using the equation $I=-\log_2 P$, where P is the corresponding probability value from Fig. 2.

Four randomization tests of pairwise independence were performed on all 741 possible pairs of characters in which: (1) characters i and j had the value of 'present,' (2) character i had the value of 'present' and character j had the value of 'absent,' (3) character i had the value of 'absent' and character j had the value of 'present' and (4) characters i and j had the value of 'absent.' Based on each test, we found that five pairs of characters were nonindependent: N7-O7, R3-P6, P6-M7, Q6-S7 and S8-Q9. Thus, characters N7, R3, Q6, M7 and Q9 were removed from our analyses because they contributed less average information than their pair.

We found that 49 (98%) of 50 whisker spot patterns contained >12.72 bits of information, which means they were reliable (for all patterns: median = 18.24 bits, range = 12.00-43.43 bits). Of the 10 000 generated patterns, 9812 (98.12%) were reliable (for all pattens: median = 18.94 bits, range = 11.61-42.43 bits) (Fig. 3). Because both proportions were $>95\%$, we feel confident in this identification method.

For the whisker spot patterns from judge 2, we found 35 characters, but removed three due to nonindependence. For the 50 patterns, the median information content was 17.67 bits (98% were reliable) and, for the 10 000 generated

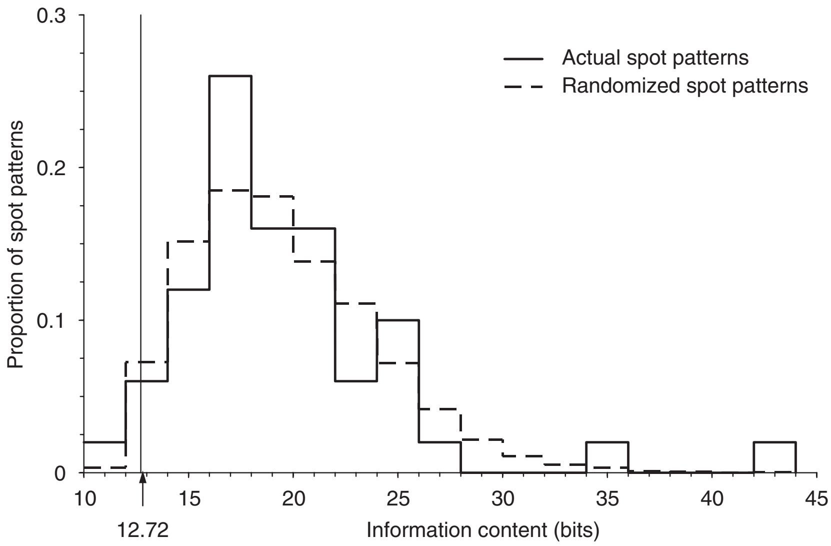

Figure 3 Probability distribution of information content for 50 polar bear *Ursus maritimus* whisker spot patterns and for 10 000 randomly generated spot patterns. The arrow indicates the minimum information content required for a pattern to be reliable.

patterns, the median information content was 17.60 bits (92.44% were reliable). For judge 3, we found 49 characters, but removed one due to nonindependence. For the 50 patterns, the median information content was 21.39 bits (100% were reliable) and, for the 10 000 generated patterns, the median information content was 22.31 bits (99.92% were reliable) (Table 1).

Discussion

Our results indicate that polar bear whisker spot patterns vary sufficiently to be used reliably to identify individuals. Thus, an identification system that takes advantage of the complexity of whisker spots will be successful. An information theoretic approach to measuring the reliability of whisker spot patterns has been used previously. For example, 23 of 25 lions could be reliably identified assuming a probability of duplication of 1% and a study population of 50 lions, but if any unusual features on the two 'substandard' lions were considered or the probability of duplication was relaxed to 1.5%, then all 25 lions could be reliably identified (Pennycuick & Rudnai, 1970). Similarly, 19 of 21 leopards could be reliably identified at a 5% probability of duplication, but only 15 at a 1% probability of duplication (Miththapala *et al*., 1989). Based on our results, 49 of 50 polar bears could be reliably identified at a 1% probability of duplication in a study population of 1000 individuals. In addition, because >95% of polar bear whisker spot patterns were reliable, we were confident in this identification method.

Table 1 Results calculated for whisker spot locations obtained from three judges who marked whisker spots on photographs of the same 50 polar bears *Ursus maritimus*

	Judge		
	1	2	3
No. of characters found	41	35	49
No. of independent characters	36	32	48
Median bits (actual)	18.24	17.67	21.39
Median bits (randomized)	18.94	17.60	22.31
% reliable (actual)	98.00	98.00	100.00
% reliable (randomized)	98.12	92.44	99.92

Differences in photograph and whisker spot selections among three judges did not affect our general results (one exception was that the proportion of reliable randomized patterns from judge 2 did not quite meet our criterion for identification utility). Different images of the same bear were sometimes taken at different angles, and so apparent positions of whisker spots varied slightly among images. Also, not all whisker spots within a pattern were equally discernible, and so where one judge selected a faint spot another judge did not. These findings suggest that when measuring the reliability of a whisker spot pattern, one must (1) work with only high-quality images of perpendicular angle and (2) clearly define what should be considered a whisker spot so that future identification by multiple observers is consistent. These results corroborate with the findings of Friday *et al*. (2000), who recommend evaluating the reliability of photographic quality and the ability of judges before using natural marks for identification.

An important difference in the derivation of characters in this study and others is that a reference row of whisker spots was used for lions (Pennycuick & Rudnai, 1970) and leopards (Miththapala *et al*., 1989) to position other spots relative to the reference row. While most polar bears clearly had three to four rows of whisker spots, we did not find a row that was consistent enough to be used as a reference. In fact, the variation in the number and spacing of spots within a row added to the complexity of each spot pattern. As a result, we used a relative coordinate system and a regular grid to determine the location of each spot. Although the use of a grid could have introduced some discrepancies into the location of whisker spots if the bear's profile was not exactly perpendicular to the camera viewpoint, the chosen grid cell size should have minimized any effect on the information content of each spot pattern.

In any identification system based on natural patterns, it is important that characters do not change over time (Pennycuick, 1978). We have at least three high-quality photographic records of known polar bears (identified through scar patterns and other body features) that have returned to our field site in different years. Qualitative observations suggest that whisker spot patterns of the same bear do not change much from year to year. However, we do not know whether whisker spot patterns in polar bears change with the bear's maturation or whether pattern similarities exist among related bears.

The use of high-quality photographs for the identification of individual whales has been shown to reduce the number of errors in photographic matching (Gowans & Whitehead, 2001). In addition, digital photography has improved the image quality and increased the efficiency of analyses in the identification of several species of dolphins (Markowitz, Harlin & Wursig, 2003). In our study, high-quality and perpendicular photographs allowed us to better discriminate between actual spots and shadows, and enabled us to discern spots that were close together. The use of digital cameras increased the number of images that could be obtained in the field, thereby increasing the probability of obtaining good photographs. Digital photographs also increased the speed at which they could be loaded into a computer for analysis while preserving their quality.

However, obtaining high-quality photographs in the field usually requires proximity to the focal animal. With our 400 mm camera lens, for example, we found that whisker spots were most distinguishable in photographs taken <50 m from the polar bear. At distances of about 75–100 m, only the largest spots were visible, and at distances >150 m, spots were too blurry to recognize. Close-up photographs of polar bears were possible because the tundra vehicle permitted us to approach bears safely. In practice, however, such flexibility is not always feasible. For example, other researchers typically observe polar bears from distances of about 200–1500 m, and usually from a fixed location (e.g. Latour, 1981*a*,*b*; Lunn, 1986; Derocher & Stirling, 1990; Dyck & Baydack, 2004). Because the reliability of identification depends on the recognition of whisker spots, we recommend using this system only with relatively high-quality photographs.

This study has shown that an identification system for polar bears based on the complexity of whisker spot patterns is reliable. The grid-based system described here could be used as an identification method, but would not be practical if whisker spots were not defined clearly or if photographs were not perpendicular to the camera viewpoint. In addition, such a system would be tedious and time-consuming if used manually. In light of our findings in this study and recent successful automated identification systems for various taxa (e.g. Kelly, 2001; Arzoumanian, Holmberg & Norman, 2005), we are developing a computer-aided identification system for polar bears based on whisker spot pattern recognition. We anticipate that this system will be useful to researchers interested in studying polar bear behavior or population parameter estimates based on capture–recapture models.

Acknowledgements

The Earthwatch Institute, Polar Bears International and the Cotswold Foundation provided funding for this study. We thank the Earthwatch volunteers who helped us in the field, our driver Bob Debits and the staff of the Churchill Northern Studies Centre for logistical support. We are especially indebted to Robert and Carolyn Buchanan for their generous assistance. We thank P.F. Quintana-Ascencio for his statistical advice and review of this paper, and our lab members, who offered helpful suggestions during the preparation of this paper. Finally, we thank two anonymous reviewers for improving the quality of this paper.

References

Arzoumanian, Z., Holmberg, J. & Norman, B. (2005). An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *J. Appl. Ecol.* **42**, 999–1011.

Borges-Landaez, P.A. & Shine, R. (2003). Influence of toe-clipping on running speed in *Eulamprus quoyii*, an Australian scincid lizard. *J. Herpetol.* **37**, 592–595.

Bretagnolle, V., Thibault, J.C. & Dominici, J.M. (1994). Field identification of individual ospreys using head marking pattern. *J. Wildl. Mgmt.* **58**, 175–178.

Derocher, A.E. & Stirling, I. (1990). Observations of aggregating behavior in adult male polar bears (*Ursus maritimus*). *Can. J. Zool.* **68**, 1390–1394.

Dyck, M.G. & Baydack, R.K. (2004). Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biol. Conserv.* **116**, 343–350.

Eckhardt, G.H. (2005). *The effects of ecotourism on polar bear behavior*. MS thesis, University of Central Florida, Orlando.

Eckhardt, G.H., Waterman, J.M. & Roth, J.D. (2002). The functional significance of play fighting in polar bears: are they asocial? *Integr. Comp. Biol.* **42**, 1224.

Eitam, A. & Blaustein, L. (2002). Noninvasive individual identification of larval *Salamandra* using tailfin spot patterns. *Amphib.-Reptil.* **23**, 215–219.

Friday, N., Smith, T.D., Stevick, P.T. & Allen, J. (2000). Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. *Mar. Mammal. Sci.* **16**, 355–374.

Gowans, S. & Whitehead, H. (2001). Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): sources of heterogeneity from natural marks. *Mar. Mammal. Sci.* **17**, 76–93.

Grinnell, J., Packer, C. & Pusey, A.E. (1995). Cooperation in male lions – kinship, reciprocity or mutualism. *Anim. Behav*. **49**, 95–105.

Hammond, P.S., Mizroch, S.A. & Donovan, G.P. (Eds) (1990). *Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters*. Cambridge, MA: International Whaling Commission.

Hayes, J.P. & Jenkins, S.H. (1997). Individual variation in mammals. *J. Mammal*. **78**, 274–293.

Jarman, P.J., Jones, M.E., Johnson, C.N., Southwell, C.J., Stuartdick, R.I., Higginbottom, K.B. & Clarke, J.L. (1989). Macropod studies at Wallaby Creek. VIII. Individual recognition of kangaroos and wallabies. *Aust. Wildl. Res*. **16**, 179–185.

Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–2862.

Kelly, M.J. (2001). Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. *J. Mammal*. **82**, 440–449.

Langtimm, C.A., Beck, C.A., Edwards, H.H., Fick-Child, K.J., Ackerman, B.B., Barton, S.L. & Hartley, W.C. (2004). Survival estimates for Florida manatees from the photo-identification of individuals. *Mar. Mammal. Sci*. **20**, 438–463.

Larson, H.J. (1982). *Introduction to probability theory and statistical inference*. 3rd edn. New York: Wiley.

Latour, P.B. (1981*a*). Interactions between free-ranging, adult male polar bears (*Ursus maritimus* Phipps) – a case of adult social play. *Can. J. Zool*. **59**, 1775–1783.

Latour, P.B. (1981*b*). Spatial relationships and behavior of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. *Can. J. Zool*. **59**, 1763–1774.

Lunn, N.J. (1986). Observations of nonaggressive behavior between polar bear family groups. *Can. J. Zool*. **64**, 2035–2037.

Markowitz, T.M., Harlin, A.D. & Wursig, B. (2003). Digital photography improves efficiency of individual dolphin identification. *Mar. Mammal. Sci*. **19**, 217–223.

Martin, P. & Kraemer, H.C. (1987). Individual differences in behavior and their statistical consequences. *Anim. Behav*. **35**, 1366–1375.

Miththapala, S., Seidensticker, J., Phillips, L.G., Fernando, S.B.U. & Smallwood, J.A. (1989). Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. *J. Zool. (Lond.)* **218**, 527–536.

Mougeot, F., Thibaul, J.C. & Bretagnolle, V. (2002). Effects of territorial intrusions, courtship feedings and mate fidelity on the copulation behaviour of the osprey. *Anim. Behav*. **64**, 759–769.

Nichols, J.D. (1992). Capture–recapture models: using marked animals to study population dynamics. *BioScience* **42**, 94–102.

Nietfeld, M.T., Barret, M.W. & Silvy, N. (1994). Wildlife marking techniques. In *Research and management techniques for wildlife and habitats*: 147–159. Bookhout, T.A. (Ed.). Bethesda, MA: The Wildlife Society.

Pennycuick, C.J. (1978). Identification using natural markings. In *Animal markings*: 147–159. Stonehouse, B. (Ed.). London: MacMillan.

Pennycuick, C.J. & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of reliability of identification. *J. Zool. (Lond.)* **160**, 497–508.

Quinn, G.P. & Keough, M.J. (2002). *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.

Regehr, E.V., Lunn, N.J., Amstrup, S.C. & Stirling, I. (2005). Population decline of polar bears in Western Hudson Bay in relation to climatic warming. In *16th Biennial Conference on the biology of marine mammals*. San Diego, CA: Society for Marine Mammalogy. p233.

Rodda, G.H., Bock, B.C., Burghardt, G.M. & Rand, A.S. (1988). Techniques for identifying individual lizards at a distance reveal influences of handling. *Copeia* **4**, 905–913.