Kelly M.J. 2001. Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. J Mamm 82(2):440-9.

Keywords: 1TZ/Acinonyx jubatus/automated photoidentification/cheetah/individual identification/ life history/method/population size/Serengeti

Abstract: Photographic identification of naturally marked animals is a powerful and non-intrusive technique for obtaining information on behavior, population size, and life-history parameters in wild populations. Yet handling large quantities of photographs is time consuming and prone to error. Computer-aided matching can limit the number of photographs that must be examined visually to confirm that 2 sightings are the same individual. To identify individuals, a 3-dimensional (3-D) computer-matching system was used to aid in matching nearly 10,000 photographs of Serengeti cheetahs, *Acinonyx jubatus,* taken over 25 years. Accuracy in matching of photographs was measured by computer-generated similarity coefficients. 3-D computer aided matching does not require familiarity with distinctive features of the particular study animal, it is robust to matcher inexperience. This technique can be modified for other species that have complex and variable pelage patterns.

COMPUTER-AIDED PHOTOGRAPH MATCHING IN STUDIES USING INDIVIDUAL IDENTIFICATION: AN EXAMPLE FROM SERENGETI CHEETAHS

MARCELLA J. KELLY*

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616

Photographic identification of naturally marked animals is a powerful and nonintrusive technique for obtaining information on behavior, population size, and life-history parameters in wild populations. Yet handling large quantities of photographs is time consuming and prone to error. Computer-aided matching can limit the number of photographs that must be examined visually to confirm that 2 sightings are the same individual. To identify individuals, I used a 3-dimensional (3-D) computer-matching system to aid in matching nearly 10,000 photographs of Serengeti cheetahs, *Acinonyx jubatus,* taken over 25 years. Accuracy in matching 2 photographs increased to 100% as the computer-generated similarity coefficient increased to 0.600 on a scale from 0 to 1. Probability of missing a match decreased to 6.4% when I used a threshold of similarity of 0.450. Poor quality of photographs decreased accuracy and resulted in up to 33% of matches being missed. Comparisons of photographs at skewed camera angles generally reduced similarity coefficients. Similarity coefficients were no higher for related or unrelated animals, suggesting that the technique is not appropriate for distinguishing subtle similarities. Because 3-D computer-aided matching does not require familiarity with distinctive features of the particular study animal, it is robust to matcher inexperience. This technique can be modified for other species that have complex and variable pelage patterns.

Key words: *Acinonyx jubatus,* automated photoidentification, cheetah, computer recognition, individual identification

Recognition of individual animals in the field was a necessary component of even the earliest studies of animal behavior and ecology (Lorenz 1937). Detailed investigation of activity patterns, courtship, mating, rearing young, movement patterns, territoriality, and sociality usually requires identification of individual animals (Delany 1978). Some information can be gleaned only through studies of known individuals. For example, studies of lifetime reproductive success of individual insects, birds, and mammals have invalidated the common assumption that all individuals have equivalent reproductive success (Clutton-Brock

1988; Newton 1989). Studies such as these generate information on reproductive variance that can now be used in predictive models of population viability (McGregor and Peake 1998). Such models also require estimates of other life-history parameters, such as survival and dispersal, which can often be obtained only from studying known individuals (Krebs 1989). For cheetahs (*Acinonyx jubatus*), individual identification was essential in determining such life-history parameters (Kelly et al. 1998), which were used subsequently in an assessment of the viability of Serengeti cheetah (Kelly 2001; Kelly and Durant 2000).

** Correspondent: mjkelly@ucdavis.edu*

Recognizing individuals in the field often

involves using naturally occurring phenotypic variation or marking animals. However, marking animals generally involves capture and handling, which risks injury to the animal (Mowat et al. 1994), can disrupt its activities and relationships to other individuals (Cuthill 1991), potentially modifies behavior and physiology (Hindell et al. 1996), can affect survivorship (Daly et al. 1992), and is not practical with large populations. Recognition by natural variation avoids these problems, and its nonintrusive nature is particularly advantageous in studies of threatened and endangered species.

Increasing numbers of long-term studies of mammals have shown that natural marks can be used to identify individuals of numerous long-lived species using a photographic file index, for example, zebras (*Equus burchelli*—Peterson 1972), giraffes (*Giraffa camelopardalis*—Foster 1966), African elephants (*Loxodonta africana*— Douglas-Hamilton 1973), lions (*Panthera leo*—Schaller 1972), chimpanzees (*Pan troglodytes*—Goodall 1986), wild dogs (*Lycaon pictus*—Frame et al. 1979), cheetahs (Caro 1994), and 27 species of cetaceans (Hammond et al. 1990a; Wursig and Jefferson 1990). In 1990, the International Whaling Commission (IWC) published a volume containing numerous studies of marine mammals that used computers to assist in matching photographs of new individuals to a long-term catalog (Hiby and Lovell 1990; Mizroch et al. 1990; Whitehead 1990). Although that IWC volume (Hammond et al. 1990a) was a landmark in the field of computer identification, new developments in computer technology and capability have been substantial since 1990. However, with few exceptions (e.g., Dott et al. 1993; Huele and de Haes 1998; Mizroch et al. 1996), such new developments and their evaluations have not been published. Additionally, no studies have used this computer technology on a terrestrial species. I used computer-assisted matching on the coat pattern of cheetahs and evaluated the effectiveness of this identification technique.

No computer-matching programs are automated completely; all potential matches (those scoring high similarity coefficients) for any species must be inspected visually to determine if 2 animals are a true match, with the final decision resting on the researcher (Whitehead 1990). Therefore, it is important to examine the accuracy of such programs and determine if they hasten the process of manually matching photographs.

Computer-matching systems can be divided into 2 types. The 1st relies on a small amount of precise data and can be characterized as a computerized version of hand sorting in which the user enters, through a keyboard, coded descriptions of such identifying features as pigment pattern, flukenotch shape, and natural marks and scar locations on a fluke map (Mizroch et al. 1990). Whitehead (1990) extended this technique by digitizing the 2-dimensional trailing edge of flukes of sperm whales (*Physeter macrocephalus*) and inputting 1 letter codes representing fluke notches, nicks, holes, and scars. Although very useful for identification, this method is sensitive to user experience and photograph quality, specifically orientation of the fluke to the camera (Carlson et al. 1990; Whitehead 1990).

The 2nd computer-aided matching technique was developed for gray seals (*Halichoerus grypus*) whose pelage patterns are more variable and complex, yet less precise, than those of most cetaceans (Hiby and Lovell 1990). This method aligns a photograph with a computerized 3-dimensional (3-D) model of the relevant body part (e.g., head and neck) allowing photographs to be processed regardless of the orientation to the camera. I used the 3-D computer-matching system on Serengeti cheetahs and tested its accuracy.

Qualitative studies of this same cheetah population have noted that similar spot patterns occur on related cheetahs (Caro and Collins 1986). Therefore, I examined if similarity coefficients produced by the matching system could be used to measure

similarities in coat patterns between related cheetahs.

MATERIALS AND METHODS

Cheetahs of the central plains of Serengeti National Park in Tanzania were photographed with 35-mm-film cameras beginning in the early 1960s until present. In 1969–1991, cheetahs at most sightings were not distinguished in the field, creating a backlog of 10,000 photographs of unidentified individuals. Because spot patterns of cheetahs are unique and remain constant through life (Caro and Durant 1991), individuals can be recognized from photographs and followed through time. However, visual identification of photographs in the field or lab can be difficult, tedious, and time consuming. Additionally, the larger the catalog of photographs, the more likely are manual errors of mismatching (Katona and Beard 1990).

I used a 3-D computer-matching system. Because the surface of the flank or head of a cheetah is nonplanar, the coat pattern changes shape with different postures or camera angles. To overcome those difficulties, Hiby and Lovell (1990, 2001) constructed a mathematical model of the surface by interpolation and contouring over a set of 3-D coordinates scattered over the flank or head. Those positions were identified originally by recognizing corresponding points, such as the shoulder and hip, on pairs of stereo photographs taken from different angles. The model was projected onto the photographic image by identifying points (e.g., shoulder and hip) whose 3-D coordinates were known, allowing the computer program to line up the 3-D model with the 2-dimensional photographic image.

I captured still images through a video camera attached to a desktop computer, although film negatives can be scanned directly into a desktop computer. Subsequently, I entered points of reference for the flank program, shoulder blade, hip joint, belly line, and backbone by tracing over them on the screen with a digitizer (Fig. 1A).

After images are digitized, a sample of the coat pattern was extracted for each animal (Fig. 1A) and stored in the computer as a matrix of numbers, consisting of gray-scale intensities read from the image, called an identifier array (IA). Similarity between different IAs was defined as the correlation coefficient between corresponding array elements, or sets of gray-scale values (Hiby and Lovell 1990). Because of error in drawing the backbone, in drawing the belly line, or in placing the hip joint, edges of different IAs did not always line up exactly. To compensate for alignment error, the computer held the 1st IA stationary while the second 1 was automatically moved 4 times up, down, right and left (Fig. 1B). The coefficient of similarity was based on the maximum correlation achieved by stretching the ''moving array'' over the ''stationary array'' 4 times. Within each of the 4 comparisons, the correlation between dark and light patterns was calculated for a number of subregions in the IA, and the average was taken (Fig. 1B). Comparison of 2 IAs took about 3 s on a desktop computer.

I found that 2 cheetahs could score different similarity coefficients depending on which was the moving versus the stationary array. For example, photograph 1 could score a 0.089 against photograph 2, and that same photograph 2 could score 0.611 against photograph 1. Differences of that magnitude (>0.450) were rare $(5%)$; more often (82% of comparisons), that difference was \leq 0.200. Therefore, I did each comparison twice (e.g., photograph 1 by 2 and photograph 2 by 1) and recorded the highest of the 2 similarity coefficients so as to further minimize error that may have resulted from misalignment of the 2 images.

I examined similarity coefficients produced by using the same cheetah photograph digitized twice at 2 different time periods separated by several weeks. I then divided perpendicular photographs (those with the cheetah flank entirely perpendicular to the camera) into 3 quality categories: excellent, moderate, and poor, based on clarity, focus, and resolution (Fig. 2). I compared the same individual cheetah to itself in 2 different photographs under all 3 quality ratings and examined the performance of the matching program. I repeated that analysis using photographs at skewed angles from the camera to determine if camera angle affected similarity coefficient. To evaluate accuracy of the system for matching cheetahs correctly and for missing matches, I visually inspected a subset of 1,000 comparisons with similarity coefficients ≥ 0.370 . That subset of comparisons contained photographs of excellent and moderate quality.

I further examined resolution of this computer program by testing if related cheetahs scored higher similarity coefficients than unrelated animals. Relatedness of individuals could be traced А

B

FIG. 1.—A) Photographs of cheetahs are digitized along the back and belly. Black arrow indicates placement of the hip joint. Sample of the coat pattern is extracted (note orange square on cheetah's flank) and is stored as a matrix of numbers called the identifier array (IA). B) The cheetah on the left (stationary array) is compared 4 times to cheetah on the right (moving array). Within each comparison, the computer searches for the maximum correlation between gray scales. The weighted average of the 4 correlation coefficients gives the overall similarity coefficient between the 2 images, in this case 0.182, as seen in the blue strip at the top of the screen.

FIG. 2.—Photographs were divided into 2 groups depending on orientation to the camera: perpendicular and skewed. Quality was then categorized as excellent, moderate, or poor depending on clarity, focus, and resolution: A) perpendicular and excellent, B) moderate and skewed, and C) perpendicular and poor. Black arrow indicates placement of the hip joint.

only through the female line because matings have rarely been observed in wild cheetahs. Maternity was established by matching photographs of small cubs who were still accompanied by their mother to adult animals later in life. I compared mothers to daughters, mothers to sons, and siblings from the same litter using photographs of excellent and moderate quality. I then examined whether the average similarity coefficient between each set of relatives was higher than the

FIG. 3.—Similarity coefficients $(\bar{X} \pm SD)$ for comparisons of A) the same cheetah photograph digitized twice, B) the same cheetah in 2 different photographs, C) cheetah mothers compared with their daughters, and D) those same mothers compared with unrelated cheetahs.

coefficient achieved by comparing that relative to an unrelated cheetah.

For comparisons of a cheetah to a relative and then a nonrelative, I used paired *t*-tests, and for all other comparisons, I used 2-sample *t*-tests (Sokal and Rohlf 1995). Statistical significance was set at $P \leq 0.05$.

RESULTS

Maximum similarity coefficients occurred in comparisons of the same cheetah photograph digitized at 2 separate time intervals, representing the high-end limits of similarity coefficients that could be achieved by the matching program. The average similarity coefficient (0.792 \pm 0.064 *SD*, range = $0.612-0.912$, $n = 94$) for cheetahs digitized twice was higher than averages for all other photographic comparisons, including comparisons of 2 different, excellent-quality perpendicular photos of the same cheetah $(0.567 \pm 0.154; t =$ 12.460, $d.f. = 148$, $P < 0.001$; Fig. 3).

Comparisons of 2 different perpendicular photographs of the same cheetah showed that excellent-quality photographs produced higher similarity coefficients than poorquality photographs (0.567 ± 0.154 versus 0.474 ± 0.146 ; $t = 3.249$, $df. = 108$, $P \le$

0.05). However, I found only a marginally nonsignificant difference between average similarity coefficients for excellent- and moderate-quality photos (0.567 ± 0.154) versus 0.487 ± 0.190 ; $t = -1.745$, $d.f. =$ 70, $P = 0.085$). No differences were found between the moderate photographs and the poor ones (0.487 \pm 0.190 versus 0.474 \pm 0.146; $t = 0.286$, $d.f. = 68$, $P > 0.05$).

For the skewed photographs, no difference in the average similarity coefficients between excellent photographs and moderate ones (0.395 \pm 0.170 versus 0.442 \pm 0.166; $t = -0.999$, $df. = 48$, $P > 0.05$) was detected, nor between excellent- and poor-quality skewed photographs (0.395 \pm 0.170 versus 0.376 ± 0.149 ; $t = 0.402$, *d.f.* $= 48, P > 0.05$). I also found no difference between similarity coefficients of skewed and perpendicular photographs of moderate quality (0.442 \pm 0.166 versus 0.487 \pm 0.190; $t = 0.790$, $d.f. = 38$, $P > 0.05$). However, skewed photographs scored significantly lower coefficients than perpendicular photographs of excellent (0.395 \pm 0.170 versus 0.567 ± 0.154 ; $t = 4.565$, *d.f.* $= 80, P < 0.001$) and poor (0.376 \pm 0.149) versus 0.474 ± 0.146 ; $t = 2.719$, $d.f. = 76$, $P < 0.01$) quality.

I calculated the accuracy of the matching program as the proportion of confirmed matches at different computer-generated similarity coefficients for perpendicular photographs of good and moderate quality combined (Fig. 4). Accuracy increased as the similarity coefficient increased. At a coefficient of ≥ 0.600 , the computer was 100% accurate in demonstrating that sightings taken at different times were from the same individuals. Accuracy dropped only slightly to 98.5% and 96.3% at the 0.550– 0.599 and 0.500–0.549 levels, respectively, for a total mismatching percentage of only 2.5% for comparisons scoring 0.500 and above. At coefficients of 0.450–0.499, slightly $>50\%$ of the comparisons were matches, an accuracy still useful in visually inspecting photographs for matches. Nearly 6.5% of comparisons of cheetahs known to

FIG. 4.—Accuracy of the 3-dimensional computer-matching system in correctly matching 2 different photographs of the same cheetah.

be the same scored < 0.450 , representing the percentage of matches missed by the computer-matching system. That percentage of missed matches increased to 33% when only poor-quality perpendicular photographs were examined.

Of those photographs that did not match, the proportion of related cheetahs in those nonmatches increased slightly as similarity coefficients increased. However, average similarity coefficients were not higher for related animals; the average mother–daughter similarity coefficient was no higher than the average coefficient between that same mother and an unrelated cheetah $(t =$ -0.411 , *d.f.* = 37, *P* > 0.05; Fig. 3). The same was true of mother–son, mother–unrelated comparisons $(t = 0.210, d.f. = 13,$ $P > 0.05$) and for sibling–sibling, sibling– unrelated comparisons $(t = -1.164, d.f. =$ 40, $P > 0.05$).

DISCUSSION

*Photograph quality.—*Photograph quality has been shown to have an effect on matching likelihood in other computer-matching programs. Whitehead (1990) found that the probability of matching increased from 59% to 80% when low-quality photographs were excluded. Unmatched photos needed to be checked visually against the catalog to be sure they were not missed matches, perhaps the greatest drawback of any

matching system (Whitehead 1990). Mizroch et al. (1990) also found that most missed matches could be attributed to poorquality photos but concluded that most matches could be found visually unless photos were extremely poor. I also found that poor-quality photographs decreased match success by increasing the probability of missing a match. Previous studies using catalog-based, computer-matching systems have classified photographs at skewed angles as poor and often unusable (Whitehead 1990). Although Hiby and Lovell (1990) claimed that the 3-D computer-matching system allowed use of photographs regardless of orientation to the camera, I found that skewed photographs generally produce lower similarity coefficients than perpendicular photographs. However, it is still worthwhile to computerize skewed and poor-quality photographs so that they can be compared with high-quality photos in the catalog to increase match success.

*Accuracy.—*The 2 potential sources of error of a computer-aided matching system are probability of matching 2 different animals as the same and missing a true match (Hammond et al. 1990b). My study found that the probability of the 3-D matching system mismatching animals was minimal. At similarity coefficients of ≥ 0.500 , the computer only occasionally (2.5%) matched 2 different cheetahs mistakenly, a value similar to that for gray seals (Hiby and Lovell 1990). Cheetahs have a complex coat pattern, only a small portion of which (the identifier array) is used in computer comparisons. Therefore, when visually confirming a match, other parts of the body can be cross-referenced, such as the tail, face, legs, or even parts of the flank outside the IA, eliminating actual mismatches. Cross-referencing is not always possible in other manual and computer-based studies that rely only on photographs of the fin, fluke, or head (cf. Hammond et al. 1990a). Doubtful matches are a particular problem for species that require a suite of photographs (sides, dorsal fins, and scars) for positive identification (Hammond et al. 1990b).

Observer continuity and memory can be valuable in long-term studies of known individuals. When 1 observer leaves, training new individuals can result in loss of information (Scott 1978). As with identifying animals in the field, studies using photographic identification have shown that experienced workers are quicker and more accurate matchers than inexperienced workers (Carlson et al. 1990; Dufault and Whitehead 1995; Scott 1978; Sears et al. 1990). The 3-D computer-aided matching technique is less susceptible to observer experience than the other type of computer-aided identification (catalog based) because 3- D computer matching does not rely on user familiarity with distinctive features used to catalog photographs. All photographs are entered, and extraction of the sample coat pattern (IA) is automated.

The probability of missing a match is more difficult to determine in identification studies. Changes in the marking pattern of an animal annually (Scott 1978) or physical scarring can cause matches to be missed by observers and computers (Carlson et al. 1990; Dufault and Whitehead 1995). In cheetahs, however, changes in coat pattern do not occur (Caro and Durant 1991). Missed matches will depend on computer performance and similarity threshold. Hiby and Lovell (1990) found that the lowest similarity coefficient that occurred between any pair of IAs from the same gray seal was slightly >0.500 . I found that many matches of cheetahs occurred between 0.450 and 0.500. Hence, I advise using a similarity threshold of 0.450 for the 3-D computermatching system for cheetahs. When the threshold of similarity was lowered from 0.500–0.450, the computer missed 6.4% of the matches. Accuracy can be further increased by including >1 photo of each known cheetah in the reference catalog; it is extremely unlikely that a cheetah will score low similarity coefficients against 2 or 3 other photographs of itself. Other com-

puter-based matching systems have not quantified percentages of missed matches for comparison.

*Speed.—*For 3-D computer matching, the time taken for an operator to enter a single cheetah photograph into the computer takes 1–3 min. Training new assistants takes about 1 h. Within several hours, a new user is nearly as fast as an experienced user. Each comparison of 2 cheetah photographs takes 2–4 s. Tens of thousands of comparisons can be run overnight. Additionally, no reliance on observer experience or memory is required.

The size of a photographic catalog and the distinctiveness of features used in identification will determine whether computer-assisted matching will hasten the process of manually matching photographs. For right whales (*Eubalaena australis*), a catalog size of about 850 animals requiring a single matching attempt of about 3 h was the maximum practical before computer assistance became desirable (Hammond et al. 1990b). These animals, however, have distinctive features, such as patterns of calluses on the head, that allow quick cataloging or dismissal of potential matches. Cheetahs have complex coat patterns usually with no particular distinctive feature; determining a nonmatch can take long, especially if photos are poor. Additionally, Sears et al. (1990) found that the probability of error was reduced when matching periods by a person were limited to 2 h; beyond that, effectiveness was limited by fatigue. I found similar results with cheetahs and suggest that computer-assisted matching can increase matching efficiency with a catalog size much smaller than 850 animals.

Similarity scores between relatives.— Caro and Collins (1986) found similarities in spot patterns on the faces and chests of related cheetahs. I also noted that particular patterns on cheetah flanks seem to resemble each other in related animals. However, related individuals did not have higher similarity coefficients than unrelated individuals in this study. This contrasts with a previous study of this same population of cheetahs in which tail bands of cheetahs from the same litter statistically resembled each other more closely than they did nonsiblings (Caro and Durant 1991).

It is possible that the 3-D computermatching system is not an appropriate method to measure subtle similarity between relatives. Only a small sample of the coat pattern is examined for correlation between dark and light patterns. This may not be a proper indication of whether 2 cheetahs share similar or repeating spot patterns over a larger part of their bodies. Conversely, it could be that tails of cheetahs exhibit measurably distinctive patterns but that flanks do not.

The 3-D computer-matching system is a very effective tool for matching large numbers of photographs for individual identification. It is accurate, fast, and robust to inexperienced matchers. This is especially important for long-term studies where the photographic catalogs increase in size over time and when researcher turnover occurs. This nonintrusive technique for identifying individuals can be modified for other species with complex and variable coat patterns on the body or face, most notably many ungulate and cat species.

ACKNOWLEDGMENTS

I thank L. Hiby and P. Lovell for developing the cheetah flank and cheetah head matching software, T. Caro for purchasing the software, and N. Pelkey for troubleshooting computer problems. T. Caro, S. Creel, M. Johnson, and 2 anonymous reviewers also provided useful comments on previous drafts of this manuscript.

LITERATURE CITED

CARLSON, C. A., C. A. MAYO, AND H. WHITEHEAD. 1990. Changes in the ventral fluke pattern of the humpback whale (*Megaptera novaeangliae*), and its effect on matching; evaluation of its significance to photoidentification research. Reports of the International Whaling Commission Special Issue 12:105– 111.

- CARO, T. M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. The University of Chicago Press, Chicago, Illinois.
- CARO, T. M., AND D. A. COLLINS. 1986. Male cheetahs of the Serengeti. National Geographic Research 2: 75–86.
- CARO, T. M., AND S. M. DURANT. 1991. Use of quantitative analyses of pelage characteristics to reveal family resemblances in genetically monomorphic cheetahs. Journal of Heredity 82:8–14.
- CLUTTON-BROCK, T. H. 1988. Reproductive success. Pp. 472–485 in Reproductive success (T. H. Clutton-Brock, ed.). The University of Chicago Press, Chicago, Illinois.
- CUTHILL, I. 1991. Field experiments in animal behaviour, methods and ethics. Animal Behaviour 42: 1007–1014.
- DALY, M., M. I. WILSON, P. R. BEHRENDS, AND L. F. JACOBS. 1992. Sexually differentiated effects of radio transmitters on predation risk and behavior in kangaroo rats *Dipodomys merriami.* Canadian Journal of Zoology 70:1851–1855.
- DELANY, M. J. 1978. Introduction: marking animals for research. Pp. 1–10 in Animal marking: recognition marking of animals in research. (B. L. F. Stonehouse, ed.). Macmillan, London, United Kingdom.
- DOTT, H., P. B. BEST, AND E. BREYTENBACH. 1993. Computer-assisted matching of right whale callosity patterns. International Whaling Commission Scientific Committee, SC/45/0 18:1–12.
- DOUGLAS-HAMILTON, I. 1973. On the ecology and behavior of the Lake Manyara elephants. East African Wildlife Journal 11:401–403.
- DUFAULT, S., AND H. WHITEHEAD. 1995. An assessment with changes with time in the marking patterns used for photoidentification of individual sperm whales, *Physeter macrocephalus.* Marine Mammal Science 11:335–343.
- FOSTER, J. B. 1966. The giraffe of Nairobi National Park: home range, sex ratios, the herd, and food. East African Wildlife Journal 4:139–148.
- FRAME, L. H., J. R. MALCOLM, G. W. FRAME, AND H. VAN LAWICK. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–1978. Zeitschrift für Tierpsychologie 50:225–249.
- GOODALL, J. 1986. The chimpanzees of Gombe: patterns of behavior. The Belknap Press of Harvard University Press, Boston, Massachusetts.
- HAMMOND, P. S., S. A. MIZROCH, AND G. P. DONOVAN (EDS.). 1990a. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. International Whaling Commission, Cambridge, Massachusetts.
- HAMMOND, P. S., S. A. MIZROCH, AND G. P. DONOVAN. 1990b. Report of the workshop on individual recognition and estimation of cetacean population parameters. Reports of the International Whaling Commission, Special Issue 12:3–17.
- HIBY, L., AND P. LOVELL. 1990. Computer aided matching of natural markings: a prototype system for grey seals. Reports of the International Whaling Commission, Special Issue 12:57–61.
- HIBY, L., AND P. LOVELL. 2001. An automated system for matching the callosity patterns in aerial photo-

graphs of southern right whales. Journal of Cetacean Research and Management Special Issue 2.

- HINDELL, M. A., M-A. LEA, AND C. L. HULL. 1996. The effects of flipper bands on adult survival rate and reproduction in the royal penguin *Eudyptes schlegeli.* Ibis 138:557–560.
- HUELE, R., AND H. U. DE HAES. 1998. Identification of individual sperm whales by wavelet transform of the trailing edge of the flukes. Marine Mammal Science 14:143–145.
- KATONA, S. K., AND J. A. BEARD. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaenangliae*) in the Western North Atlantic Ocean. Reports of the International Whaling Commission, Special Issue 12: 295–305.
- KELLY, M. J. 2001. Lineage loss in Serengeti cheetahs: consequences of high reproductive variance and heritability of fitness on effective population size. Conservation Biology 15:137–147.
- KELLY, M. J., AND S. M. DURANT. 2000. Viability of the Serengeti cheetah population. Conservation Biology 14:786–797.
- KELLY, M. J., ET AL. 1998. Demography of the Serengeti cheetah population: the first 25 years. Journal of Zoology (London) 244:473–488.
- KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York.
- LORENZ, K. 1937. Imprinting. The Auk 54:245–273.
- MCGREGOR, P., AND T. PEAKE. 1998. The role of individual identification in conservation biology. Pp. 31–55 in Behavioral ecology and conservation biology (T. M. Caro, ed.). Oxford University Press, New York.
- MIZROCH, S. A., J. A. BEARD, AND M. LYNDE. 1990. Computer assisted photo-identification of humpback whales. Reports of the International Whaling Commission, Special Issue 12:63–70.
- MIZROCH, S. A., R. HOBBES, D. MATTILA, L. S. BARAFF, AND N. HIGASHI. 1996. A new survey protocol for capture-recapture studies in humpback whale winter grounds. International Whaling Commission Scientific Committee, SC/48/0 18:1–14.
- MOWAT, G., B. G. SLOUGH, AND R. RIVARD. 1994. A comparison of three live capturing devices for lynx, capture efficiency and injuries. Wildlife Society Bulletin 22:644–650.
- NEWTON, I. 1989. Lifetime reproductive success in birds. Academic Press, San Diego, California.
- PETERSON, J. C. B. 1972. An identification system for zebra (*Equus burchelli* Gray). East African Wildlife Journal 10:59–63.
- SCHALLER, G. B. 1972. The Serengeti lion. The University of Chicago Press, Chicago, Illinois.
- SCOTT, D. K. 1978. Identification of individual Bewick's swans by bill patterns. Pp. 160–168 in Animal marking: recognition marking of animals in research (B. Stonehouse, ed.). Macmillan, London, United Kingdom.
- SEARS, R., J. M. WILLIAMSON, F. W. WENZEL, M. BE-RUBE, D. GENDRON, AND P. JONES. 1990. Photographic identification of the Blue Whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. Reports of the International Whaling Commission, Special Issue 12:335–342.

- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W. H. Freeman and Company, New York.
- WHITEHEAD, H. 1990. Computer assisted individual identification of sperm whale flukes. Reports of the International Whaling Commission, Special Issue 12:71–77.
- WURSIG, B., AND T. A. JEFFERSON. 1990. Methods of photo-identification for small cetaceans. Reports of the International Whaling Commission, Special Issue 12:43–52.

Submitted 20 March 2000. Accepted 5 September 2000.

Associate Editor was Ronald E. Barry.