HELBIG, A. J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating Blackcaps (*Sylvia atricapilla*). Behav. Ecol. Sociobiol. 28:9–12.

HOLLEBACK, M. 1974. Behavioral interactions and the dispersal of the family in Black-capped Chickadees. Wilson Bull. 86:466–468.

HUSBY, M., AND T. SLAGSVOLD. 1992. Post-fledgling behaviour and survival in male and female magpies *Pica pica*. Ornis Scand. 23:483–490.

LINDÉN, M., L. GUSTAFSSON, AND T. PÄRT. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. Ecology 73:336–343.

MAGRATH, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. J. Anim. Ecol. 60:335–351.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 18:453–487.

MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the Northern Wheatear (*Oenanthe oenanthe* L.). Auk 101:741–752.

NORTON-GRIFFITHS, M. 1969. The organization, control and development of parental feeding in the Oystercatcher (*Haematopus ostralegus*). Behaviour 34:55–114.

PAYNE, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8:1–28.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Ann. Rev. Ecol. Syst. 21:481–508.

ROYAMA, T. 1966. Factors governing feeding rate, food requirements and brood size of nestling Great Tit *Parus major*. Ibis 108:313–347.

SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin, TX.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd edn. W. H. Freeman, New York.

SOLER, M. 1990. Relationship between the Great Spotted Cuckoo, *Clamator glandarius*, and its corvid hosts in a recently colonized area. Ornis Scand. 21:212–223.

SOLER, M., AND J. J. SOLER. 1991. Growth and development of the Great Spotted Cuckoos and their magpie host. Condor 93:49–54.

SOLER, M., J. J. SOLER, AND J. G. MARTINEZ. In press. Sympatry and coevolution between the Great Spotted Cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host. *In* S. I. Rothstein [ed.], Evolution and ecology of brood parasitism.

STEYN, P. 1973. Some notes on the breeding biology of the Striped Cuckoo. Ostrich 44:163–169.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). J. Anim. Ecol. 58:275–286.

WOODWARD, P. W. 1983. Behavioral ecology of fledgling Brown-headed Cowbirds and their hosts. Condor 85:151–163.

WYLLIE, J. 1981. The cuckoo. B. Y. Batsford, London.

The Condor 96:805–809

A TECHNIQUE FOR MEASURING PRECOCIAL CHICKS FROM PHOTOGRAPHS[1]

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Key words: American Coot; Fulica americana; *body size; distance; growth rate; nidifugous chicks; photography.*

Measures of the body size and growth rate of chicks are central to many avian studies (Ricklefs 1983). In some species, growth rate or body size at fledging is correlated with subsequent recruitment into the population (Perrins 1965), indicating that these measures can be important indices of fitness. In nidicolous birds, measures of nestling body size can be obtained simply by visiting nests. However, obtaining growth data for the nidifugous young of precocial birds is often far more difficult. Here I describe a technique for estimating the size of objects in photographs and show how this technique can be used to obtain size and growth measures for chicks, especially the swimming chicks of aquatic species that can be approached with floating blinds (Nuechterlein 1982). I then demonstrate the accuracy and utility of this method using data collected from both captive and free-ranging American Coot (*Fulica americana*) chicks.

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ESTIMATING THE SIZE OF AN OBJECT IN A PHOTOGRAPH

Two things are needed to estimate the size of an object in a photograph: (1) the distance at which the object was photographed and (2) a regression equation for predicting the magnification of objects in photographs as a function of distance photographed, specifically for the particular lens that is used. Here, magnification of an object in a photograph refers to size of the object in the photograph relative to the object's true size.

The relation between the magnification of an object in a photograph and the distance it was photographed at can be obtained by (i) photographing a known-sized object at various measured distances, (ii) measuring the size of the object in each photograph or projected image, (iii) dividing measured size by true size to obtain the magnification of the object at each distance, and (iv) performing regression analysis to obtain a predictive relationship between magnification and distance photographed. This regression equation can then be used to predict the magnification of an object in a photograph taken at a known distance; the actual size of the object is the size measured on the photographic image divided by the magnification. It is critical to note, however, that the regression equation will only predict the magnification of objects in photographs printed or projected at the same photographic enlargement as the photographs used to obtain the regression (photographic enlargement is the size of the total photographic image relative to negative or slide size). Moreover, each regression is specific to a particular lens and researchers will have to obtain their own regression equations.

To determine the relation between the distance at which an object is photographed and its magnification in the photograph, I photographed a 10 cm × 1 cm rectangle, drawn on a flat manila folder, at 10 measured distances between 2.5 m to 15 m. I used a 300 mm lens and Kodachrome 64 slide film. I then measured the size of the projected image of the rectangle on a photographic screen. Dividing each projected size by the real size (10 cm) yielded the magnification of the image. The magnification of an object in an image should be a function of the inverse of the photographic distance, rather than actual photographic distance, so I plotted magnification as a function of the inverse of distance. A polynomial regression gave the best fit and the relation was extremely tight (Fig. 1; $F = 6.71 \times 10^{18}$, df = 2, 7, $P < 0.001$, adjusted $R^2 = 1.00$).

I next took test photographs of the 10 cm long rectangle at various measured distances between 2.5 and 9 m, measured the size of the rectangle on projected images, and used the regression to predict the actual size of the rectangle. These predicted size estimates were accurate and the average error in estimated size, expressed as a percentage of true size, was 0.24 ± 0.03%, $n = 31$ estimates. This high accuracy was achieved under ideal conditions where the distance to the object could be measured accurately. In field conditions, especially where photographing mobile animals, it would not be possible to measure the distance between the animal and the camera directly with a measuring tape. I therefore outline a technique for estimating the distance to objects using a telephoto lens as a rangefinder, and then demonstrate the utility of combining this technique with one described above.

ESTIMATING THE DISTANCE TO AN OBJECT USING A TELEPHOTO LENS

Camera lenses have "distance to object in focus" markings on the focusing ring and these markings permit a rough estimate of the distance to a subject that is in focus. To increase the precision of the markings on the barrel of the 300 mm lens I used, I placed a piece of tape on the focusing ring and marked the tape with the following distance intervals; 0.5 ft divisions between 12 and 15 ft, 1.0 ft divisions between 15 and 30 ft, and 2.0 ft divisions between 30 and 50 ft. The location of each distance marker was determined by focusing on an object at a precisely measured distance from the film plane and I used non-metric intervals because I did not have access to a metric tape measure.

To determine the accuracy of this "rangefinder," I estimated distance by focusing on an object and reading the distance markings on the focusing ring while an assistant measured the actual distance with a measuring tape. The camera was attached to a tripod to increase stability and ease of focusing. The distance estimates I obtained were very accurate. The mean error (absolute value of measured distance minus estimated distance), expressed as a percentage of the measured distance, was 0.89% ± 0.08% ($n = 93$). The error also increased slightly with distance; Error (%) = 0.08 Distance (m) + 0.30, $F = 15.39$, df = 1, 91, $P < 0.001$. With an average error of less than 1% over the range of distances tested, this method clearly permits an accurate distance estimate. This accuracy, in combination with the precise relation between distance and object magnification, should make it possible to obtain an accurate size estimate from a photograph when the distance to the object is estimated rather than measured directly.

TESTING THE ACCURACY OF BOTH METHODS COMBINED

I performed three tests to assess how accurately the size of an object can be estimated from photographs when the distance to the object is estimated using the camera lens as a rangefinder.

(1) Inanimate object of known size. I photographed the 10 cm rectangle at randomly chosen distances between 2.5 and 9 m and estimated the distance to the rectangle using the markings on the focusing ring. I later measured the size of the projected images of the rectangle and, with the regression equation derived above (Fig. 1), used the distance estimates to predict the magnification and actual size of the rectangle in each slide. The predicted size estimates were accurate; mean error was 0.94 ± 0.14% of the actual size ($n = 31$ estimates). The accuracy of the estimate also decreased with distance; Error (%) = 0.14 Distance (m) + 0.16, $F = 4.91$, df = 1, 29, $P = 0.035$.

This trial was run under ideal conditions because the object being measured was an immobile, flat drawing maintained perpendicular to the camera. Animals are not usually so cooperative, so I assessed the accuracy of the technique in estimating body size of both captive and wild coot chicks.

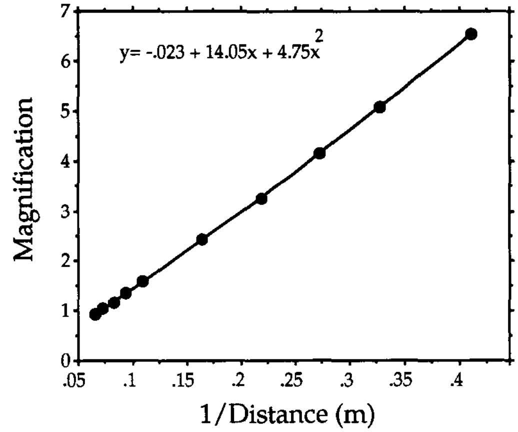

FIGURE 1. Example of the magnification of an object in a photographic image as a function of the inverse of the distance at which the object was photographed.

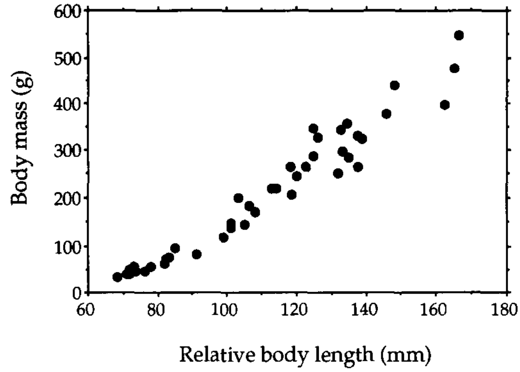

FIGURE 2. The relation between the body mass of American Coot chicks and their relative body length. Relative body length is the size measured on the photographic image.

(2) Captive American Coot chicks. I raised 11 chicks in captivity in 1988 and photographed them every three or four days while they swam in a small wading pool. I obtained photographs of chicks ranging in age from 8 to 50 days and ranging in body mass from 26 to 550 grams. All chicks were photographed with a 200 mm lens from a set distance of 10 feet, as indicated by the manufacturer's markings on the lens barrel. I preset the focusing distance and then altered the camera position to bring the chicks into focus. I used black and white film and on each image projected from a darkroom enlarger, I measured the body length of the swimming chick at the waterline. Since all chicks were photographed from the same distance, I used relative body length in this trial rather than actual length. Relative length is the size of the chick on the projected image. Most chicks were photographed twice in each session to allow for a repeatability calculation (Falconer 1981, Lessels and Boag 1987).

The measures of relative body length had a high repeatability (Table 1). Photographs varied greatly in quality and some images were difficult to measure. To assess the effect of photograph quality on repeatability, I ranked the quality of each image into three arbitrary categories: (i) Excellent = sharp focus and a perpendicular body orientation, (ii) Good = slightly out of focus chick or body oriented slightly away from perpendicular, and (iii) Poor = badly out of focus and/or body orientation considerably away from lateral. Omitting the small number of Poor rank photographs from the calculation did not affect the repeatability, but the repeatability based solely on Excellent rank photographs was slightly higher (Table 1).

"Body length at waterline" is not a standard measure of body size so I examined the relation between body length at waterline and body mass, a more typical measure of body size. Each chick was weighed within 4 hr of being photographed, and where chicks were photographed more than once on a given day, I used the average of the length estimates. Body length on a photograph is highly correlated with body mass (Fig. 2; Pearson correlation $r = 0.97$, $n = 43$, $P < 0.001$) and is thus a biologically meaningful measure of body size.

(3) Wild American Coot chicks. I obtained body size

TABLE 1. Repeatabilities of body size measures obtained from photographs of American Coot chicks. Repeatabilities are based on analysis of variance (Lessells and Boag 1987).

	Size measure	Quality of photographs included*	Repeatability	F ratio (df)†
I. Captive chicks	Body length	all	0.980	112.33 (30, 41)
		E, G	0.980	115.51 (24, 33)
		E	0.986	152.45 (8, 10)
II. Wild chicks	Body length	all	0.694	6.51 (49, 72)
		E, G	0.806	10.94 (49, 70)
		E	0.824	11.49 (49, 62)
	Culmen	all	0.681	5.83 (49, 62)
		E, G	0.683	5.83 (49, 62)
		E	0.792	9.18 (31, 37)

* E = excellent, G = good, P = poor (see text).
† P for all F tests < 0.001.

estimates for wild coot chicks during a study of parental care in central British Columbia in 1992 (Lyon et al., unpubl. ms.). Broods were followed in a floating blind, and swimming chicks (n = 198) were photographed with a 300 mm lens. As described above, I estimated the distance from which each photograph was taken. I later projected each photograph on a screen, measured the body length at waterline of each chick, and converted these measures to estimates of actual body length with the regression shown in Figure 1. All but two of the 552 photographs were taken at a distance of less than 10 m, and the average photographic distance was 5.84 m ($\pm$0.063 m). All chicks were individually color marked within broods. No chick was photographed on more than one day (i.e., each chick was photographed at only one age), but the ages of chicks photographed ranged from 19 to 54 days.

Many chicks were photographed two or more times so it is possible to calculate repeatabilities for the body size estimates. I also examined the effect of photograph quality on the repeatability of body measures, as was done for the captive chicks. To calculate repeatability in each case, I excluded chicks represented by a single photograph and then randomly chose 50 chicks from the remaining pool of chicks. The estimates of body length had high repeatabilities (Table 1). Removing Poor photographs increased repeatability markedly, but there was little increase in repeatability when Good photographs were also excluded (Table 1). I also examined the repeatability of a second measure of body size, culmen length. As before, I chose 50 chicks at random from the pool of available chicks represented by at least two photographs, except in the trial restricted to "Excellent" photographs, where only 32 chicks were represented by two or more photographs. Repeatabilities of culmen length were also high, and excluding both "Poor" and "Good" quality photographs improved the repeatability noticeably (Table 1).

DISCUSSION

It is clear that useful size measurements of objects can be obtained from photographs taken at known, or accurately estimated, distances. These measures of body size are not meant to be a substitute for the accurate body size measures needed for some studies. Nonetheless, the high repeatabilities of these measures suggest that they will be useful for studies geared for detecting strong ecological patterns. This technique complements a method described by Butler et al. (1990) for measuring objects with a telescope. Their method requires that the object sit motionless for a few seconds while size can be estimated from a micrometer eyepiece. Moreover, it is also necessary to measure or accurately estimate the distance between the animal and the telescope. Clearly, this method will not be appropriate for subjects, like precocial young, that move constantly or wherever the distance to the subject cannot be estimated accurately. The photographic method I describe circumvents these problems and can be used for any subject that can be approached fairly closely. It should be particularly useful for obtaining relative indices of growth for aquatic birds with precocial young that can be approached with floating blinds, and these include loons, grebes, and waterfowl. My method has the added advantage of providing a permanent photographic record; moreover, measurement error can be reduced by eliminating low quality photographs from the analyses.

The repeatabilities of body length for captive chicks were much higher than those obtained for wild chicks (Table 1), and possible reasons for this difference should be mentioned. I believe that differences between the two trials in the accuracy of distance estimates were probably the most important factor. With the captive chicks, the distance to subject was maintained constant for all photographs. By contrast, distances were variable for the wild chick data set and two factors may have resulted in inaccurate distance estimates. First, the chicks were photographed from a small hole in the blind covering and I had to pull the camera back into the blind to read the distance markings on the lens barrel for each photograph. Pulling the lens back through the opening of the blind may have sometimes caused the lens barrel to rotate away from the focusing position in which the photograph was taken. This source of measurement error could be eliminated with a device that locks the lens into a fixed position when a photograph is taken. A second source of inaccuracy in estimating the distance to the subject is error in reading the distance markings on the lens barrel. Some broods were difficult to approach or remained hidden in the vegetation for long periods of time, and I often had to work quickly to photograph several chicks when I finally succeeded in getting a clear view of the brood. The need for haste may have caused me to incorrectly read the distance markings on the lens barrel. This problem could be reduced if the markings were color-coded so that major intervals (e.g., 5, 10, 15, . . .) could not be confused. Measurement error can be further reduced by photographing each animal or object several times and using the mean value for each individual and, further, by eliminating outlier measurements that differ from the mean value by more than some predetermined amount.

I have demonstrated the utility of using photographs to measure the body size of chicks, but this method can be used to measure the size or area of any objects than cannot be measured directly (e.g., structural size of large birds, large mammals, prey sizes for raptors or piscivores). Similarly, I have shown that a telephoto lens can be used to measure distances to objects in cases where direct distance measurements are not possible, and possible candidates include the height of nests above the ground or the minimum distance that parent birds approach a human observer in studies of nest defense (e.g., Montgomerie and Weatherhead 1988).

Susie Everding, Caroline Morrill and Louise Cargill helped raise the captive chicks and John Eadie and Linda Hamilton helped with the study of wild chicks. John Eadie and Tim Karels measured the photographs of the wild chicks. The measures of captive chicks were obtained during a study of brood parasitism funded by a NSF Doctoral Dissertation Improvement Grant and the measurements of wild chicks were done as part of a study funded by a N.S.E.R.C. (Canada) operating grant to John Eadie. Comments from Linda Hamilton, Geoff Hill, Erica Dunn and an anonymous reviewer improved the manuscript.

LITERATURE CITED

BUTLER, R. W., A. M. BREAULT, AND T. M. SULLIVAN. 1990. Measuring animals through a telescope. J. Field. Ornithol. 61:111–114.

FALCONER, D. S. 1981. Introduction to quantitative genetics, 2nd ed. Longman, London.

LESSELS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defense by parent birds. Quart. Rev. Biol. 63:167–187.

NUECHTERLEIN, G. L. 1982. Birds that walk on water. Natl. Geogr. Mag. 161:624–637.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major* L. J. Anim. Ecol. 34:601–647.

RICKLEFS, R. E. 1983. Avian postnatal development, p. 1–83. *In* D. S. Farner and J. R. King [eds.], Avian biology, vol 5. Academic Press, New York.

The Condor 96:809–812

VARIATION IN PARENTAL CARE WITH OFFSPRING AGE IN THE GREATER FLAMINGO[1]

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Key words: Age; Greater Flamingo; parental care; Phoenicopterus ruber roseus.

Several studies have predicted how parental investment should change in relation to the age of offspring (Williams 1966, Winkler 1987). The Reproductive Value Hypothesis (RVH) states that parents should be prepared to invest more in older juveniles because they have a higher probability of surviving to breeding age. This may occur because older juveniles are closer to maturation and because the instantaneous rate of juvenile mortality generally decreases with increasing age (Clutton-Brock 1991). Increase in feeding effort with chick age has been documented for some species of colonial waterbirds. In Pigeon Guillemots (*Cepphus columba*) provisioning rates increased with chick age, only during the first part of the nestling period (Emms and Verbeek 1991). Feeding rates were not observed to vary with chick age in the closely related Black Guillemot (*Cepphus grylle*), but size of fish delivered to the nest increased with chick age (Cairns 1987). As chicks grow older they also have greater food requirements, and increased parental care might simply correspond to the higher energetics and nutritional demands of the offspring. Further evidence for increased parental care with increasing age of offspring comes from studies of brood defense. Brood defense has been reported to increase with nestling age in several passerine species (Andersson et al. 1980, Redondo and Carranza 1989, but see Knight and Temple 1986, Westmoreland 1989).

However, the observed increase in parental care with offspring age can also be influenced by confounding variables such as parental age and or quality. Breeding success is known to increase with parental age in several bird species (Saether 1990) and this can be the result of increased experience with age. In addition, as parents grow older, their potential for future reproduction decreases. Thus the cost of reduced future reproductive success should decline with age and older parents should be selected to invest more in offspring compared to younger parents (Pugesek 1981). Therefore, it is important to control for parental age when considering variation in parental care with offspring age.

Here, we analyze data from two years on the duration of feeding bouts by Greater Flamingo (*Phoenicopterus ruber roseus*) parents of known age and sex to their offspring. We show that only male parental care increases with offspring age. We discuss our results in relation to lifetime reproductive success and costs of reproduction.

METHODS

The Greater Flamingo is a filter-feeder that breeds in dense colonies often numbering several thousands of pairs. Females lay a single egg and both parents share incubation. Flamingos have bred intermittently in the saline lagoons of the Camargue in southern France for centuries (Johnson 1983). In every year since 1972, they have bred in the Etang du Fangassier, part of the large complex of commercial salt pans of Salin de Giraud. On average, since 1977, 12% of the chicks have been banded each year with darvic rings engraved with alphanumeric codes (Johnson 1989).

Birds start to gather at the breeding site in March. Egg laying usually begins in April and continues for four to six weeks. At about 10 days of age the chicks

[1] Received 17 August 1993. Accepted 3 February 1994.