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Sources of bias in observations of Murre provisioning behavior

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ABSTRACT. Although many studies involve observations of parent birds feeding their young, few investigators have attempted to quantify possible sources of bias associated with such observations. To address this issue, we observed the provisioning behavior of Thick-billed Murres (*Uria lomvia*) at a breeding colony on Coats Island, Nunavut, Canada from 2004 to 2007. We also attached electronic recorders that indicated every return to the colony and, for some prey items, allowed us to determine whether they were correctly identified based on the profile of the dive preceding delivery. We recorded when the bird arrived without a fish and, because our electronic recorders did not impact feeding rates, we were able to convert the number of arrivals into feeding rates. Of 3744 arrivals observed by the recorders, 13% of arrivals were missed by the observers at the colony, 13% were unidentified and 5% were misidentified. The proportion of missed feedings (AIC weight = 0.46) and unidentified prey (AIC weight = 0.48) increased with decreasing light level, whereas the proportion of misidentified prey increased with increasing light level (AIC weight = 0.30). Distance from the observation blind to the breeding site also influenced the proportion of missed feedings. Unidentified and misidentified feeds occurred more often when the breeding site was partially obscured. Unidentified prey also varied with observer ($P = 0.0005$), although this did not correlate with observer experience. Fish lengths recorded by observers viewing photographs of fish subsequently collected, and therefore of known length, were consistently about one centimeter lower than actual fish length ($R^2 = 0.71$). After correcting for missed feeds and misidentification of fish lengths, we obtained robust estimates of chick energy intake rates (accuracy ± 2%). We concluded that light level was the largest source of bias in feeding watches, but that other factors, such as breeding site location, needed to be considered when analyzing data collected from these watches.

SINOPSIS. **Fuentes del diagonal cuando observan la alimentación de jóvenes para *Uria***

Aunque una práctica común en ornitología es observar lo que alimentan los aves a sus jóvenes, pocos estudios cuantifican el diagonal asociado al procedimiento. Para abordar este problema, condujimos 14 "observaciones de alimentación" (24 o 48 hr) en una colonia de araos de Brünnich (*Uria lomvia*) a Coats Island, Nunavut, 2004–07. También atamos los registradores de la tiempo-profundidad-temperatura que permitieron de registrar cuando los aves llegan a la colonia y, para algunos artículos de presa, para determinar si fueron identificados correctamente basados en el perfil de zambullida. Registramos cuando el ave llegó sin un pescado (demostrado previamente que la misma proporción de aves entrega pescados con y sin los registradores), podíamos convertir el número de entregas en número de alimentaciones. De 3744 alimentaciones observadas, no registramos 13% de alimentaciones, no podemos identificar 13% y identificamos malas 5%. La proporción de alimentaciones que no registramos (AIC weight = 0.46) y no identificamos (AIC weight = 0.48) aumentó con el nivel de luz bajado, pero la proporción de alimentaciones identificamos malas diminuó con el nivel de luz bajado. La proporción de alimentaciones que no registramos aumentó con distancia de la observación al nido. La proporción de alimentaciones que no podemos identificar y que identificamos malas aumentó cuando el nido fue obscurecido parcialmente. La proporción de alimentaciones que no podemos identificar varió con el observador (P = 0.0005), aunque no ésta correlacionara con experiencia del observador. Las tamañas de los pescados registradas por los observadores que veían las fotografías de los pescados eran constantemente cerca uno centímetro más bajo ($R^2 = 0.71$). Concluimos que el nivel de luz era la fuente más grande de diagonal en relojes de alimentación, pero que otros factores, tales como localización del nido, necesitaron ser considerados cuando analizan datos de estos observaciones.

Key words: Brünnich's Guillemot, feeding watch, observational bias, observer fatigue, Thick-billed Murre, *Uria lomvia*

Understanding bias is an important part of accurately quantifying observations in field or-

nithology (Borberg et al. 2005, Powell et al. 2005). Sources of bias in field ornithology include observer experience or ability (Bart and Schoultz 1984, Sauer et al. 1994, Carss and Godfrey 1996, Kendall et al. 1996), time of day (Robbins 1981), distance between the observer

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and the bird (Somershoe et al. 2006), habitat structure (Bart et al. 1995, Keller and Scallan 1999), and duration of observations (Gaston and Noble 1985). In many cases, researchers ignore bias, implicitly hoping that biases occur randomly and contribute to noise in such a way that, with a large enough sample size, the "signal" of interest can still be detected. Nonetheless, when quantified, bias is often significant and systematic (Cézilly and Wallace 1988, Thomas and Martin 1996, Gonzales-Solis et al. 1997). With appropriate quantification of sources of bias, correction factors can sometimes be developed that statistically remove or reduce bias (Link and Sauer 1996, Thomas and Martin 1996, Borberg et al. 2005).

Investigators have examined provisioning behavior and quantified the types of food delivered to nestlings in a wide variety of birds, including raptors (Dykstra et al. 2003, Harmata et al. 2007), songbirds (Williams 1987, Nolan et al. 2001), seabirds (Davoren and Montevecchi 2003, Gaston et al. 2003), and waders (Lombardini et al. 2001, Figueroa and Stappung 2003). Although cameras are increasingly used, visual observations continue to be used in many such studies (Dykstra et al. 1998, Stillman et al. 2002, Gill and Elliott 2003), especially studies of colonial species where an observer can monitor more nests than a camera (Davoren et al. 2003, Baillie and Jones 2004, Hipfner et al. 2006). However, few investigators have attempted to quantify the uncertainty associated with visual observations of feeding rates and types of food delivered.

During feeding observations, errors may arise because (1) feedings may be missed (Harris 1984), (2) a feeding is observed, but the delivery location (e.g., nest site number) or food type (Margalida et al. 2005) may not be determined, and (3) an incorrect food type may be recorded (Cézilly and Wallace 1988, Gonzales-Solis et al. 1997). Detecting bias due to (1) and (3) is difficult because it is difficult to derive second, independent measurements of feeding rates or food identity. To address bias arising from missed feeding visits, we attached temperature-depth recorders (TDR) to Thick-billed Murres (*Uria lomvia*) and simultaneously conducted feeding observations to provide an independent index of the number of times birds visited the colony. Because we recorded when birds arrived without a prey item and feeding rates were similar for

birds with and without recorders (Elliott et al. 2007, 2008b), we were able to convert the number of arrivals into feeding rates. To address bias associated with (3), we used TDR profiles to determine probable prey types and also had observers identify photographs of prey of known identity from brief glimpses of the pictures. Grouping procedures (Cooper et al. 1990) and quantitative analyses undertaken (Sherry 1990) can also lead to biases, and we examined several different mathematical procedures for converting information collected from visual observations of feeding rates into energy delivered to the chick.

The tendency to make each of the three potential errors listed above may be influenced by: (1) observer ability, (2) observer fatigue, (3) food delivery rates, (4) light levels, and (5) nest location. Our objective was to examine the effect of each of these five potential sources of bias on the accuracy of visual observations of the provisioning behavior of adult Thick-billed Murres.

METHODS

We observed Murres from a blind at the Coats Island, Nunavut, Canada (62°57′N, 82°00′W; Gaston et al. 2005) from 20 July to 10 August 2004–2007. Our techniques and conditions were typical of those used in previous studies at our study site (Gaston et al. 2003, Hipfner et al. 2006, Elliott et al. 2008a, b). Murre breeding sites are 1–5 m below the blind, and darkness occurs between about 22:00 and 4:00 at our study site (Croll et al. 1992). Most observations were 3 h in duration per observer, but varied from 30 min to 8 h. Observers were asked to record the time of all arrivals at the colony, whether a prey item was delivered and, if so, the type of prey, the band combination of the bird making the delivery, whether the bird remained at the colony or left, and the time the bird left. Observers noted when a prey item was unidentified and, if so, described it in as much detail as possible. Birds returning without prey were also recorded. All new observers made extensive casual observations and received >1 h training with an experienced observer. Observers were also shown photographs and specimens of typical prey types. Photographs of potential prey items and maps of the study area showing breeding site numbers were available in

the blind so they could be referred to during observations.

Missed arrivals. We attached 4.5-g TDR (Lotek LTD 1100, St. John's, Newfoundland; 24 in 2004, 33 in 2005, 57 in 2006, and 36 in 2007; sample interval = 3 s) to the legs of Thick-billed Murres whose feeding behavior was being monitored. TDR were usually attached at least 30 min prior to feeding watches, and the breast of birds with TDRs was marked with a permanent marker to facilitate identification. Temperature readings at the colony were always higher than during flight, so arrival times were readily identifiable based on the temperature log (Tremblay et al. 2003, Elliott et al. 2007, 2008a,b; Fig. 1) and provided an independent index of arrival rates. The time on observers' watches was synchronized within 1 min to the time used by the TDRs. We examined the temperature logs for each Murre and the log for each feeding observation to determine if arrivals were observed or missed. Because there is no loafing away from the breeding site during the chick-rearing period (Gaston and Noble 1985), all colony visits recorded by TDRs occurred at the breeding site. In contrast to back-mounted TDRs (14–35 g; Watanuki et al. 2001, Hamel et al. 2004, Paredes et al. 2004), our smaller, leg-mounted 4.5 g TDRs had no impact on provisioning rates or trip duration (Elliott et al. 2007, 2008). Consequently, the rate of missed arrivals obtained from the TDRs is likely representative of the population as a whole. We assumed that arrivals with and without food were equally likely to be missed, so that the proportion of missed arrivals was equal to the proportion of missed feeds.

Misidentified prey. Elliott et al. (2008b) found that some prey (excluding capelin [*Mallotus villosus*], cod [*Boreogadus saida*], and sculpin [*Triglops* sp.]) could be identified with 95% certainty by dive behavior preceding their delivery. For example, pelagic prey items were usually associated with V-shaped dives and benthic prey items with U-shaped dives (Elliott et al. 2008b). Occasionally, prey items were reported following apparently atypical behavior (i.e., a shallow water item was reported following a deep dive or a benthic prey item following a V-shaped dive). For example, Murres typically delivered sandlance (*Ammodytes* sp.) following flights of short duration and shallow dives, but a single observation clumped with several morphologically similar capelin observations with long flight times and deep dives (Elliott et al. 2008b). We assumed that most mismatches between
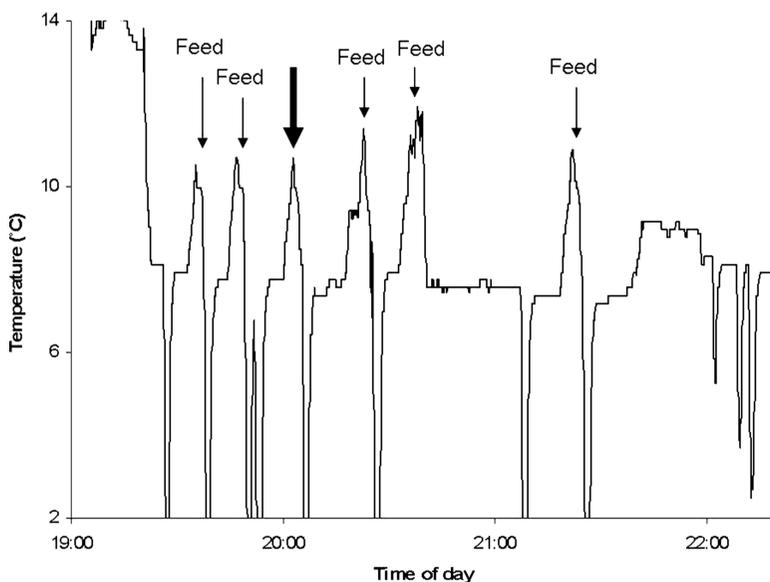

Fig. 1.   Temperature reading, as displayed in the Lotek GUI, for a Thick-billed Murre at Coats Island, Canada, on 7 August 2006. The small arrows denote feeding visits as recorded by the observer at the colony. The large arrow represents a missed feeding. Air temperature, as shown by the flight just before 23:00, and recorded on a thermometer at camp at 20:00, was about 9°C.

prey identification and dive behavior represented prey misidentifications, and used "deliveries that fall outside of their 95% Minimum Convex Polygon on the Multigroup Discriminant Analysis" (Elliott et al. 2008b) as an index for misidentification.

To examine misidentification of fish size, we presented experienced ($N = 4$) and inexperienced ($N = 8$) observers with photographs of prey deliveries where the size of the fish had been determined either by obtaining the specimen or by a calculation based on the position of the fish's fins relative to the end of the bill, in comparison to a size range of actual specimens ($N = 50$; Larson and Craig 2006).

Analyses of bias. Using R 2.4.1 (CRAN 2007), we considered the following as dependent variables in a general linear model (binomial family; logit link): (1) missed feedings, (2) unidentified prey, and (3) index of misidentified prey. Independent factor variables were: (1) observer experience (0 = no previous experience, and $1 = \geq 3$ yr of experience; no observers had 1–2 yr of experience), and (2) site visibility (0 = site obscured, and 1 = site slightly obscured or bird delivers facing away from the blind). Independent continuous variables were: (1) time since the start of the watch, (2) time since the last recorded delivery, (3) time of day (cosine-transformed around 01:00 to harmonize with light levels), and (4) distance to the site. We used AIC scores computed by R to rank different models (Anderson et al. 2000, Burnham and Anderson 2001). We used a stepwise procedure starting with the global model (all terms and all two-way interaction terms) and removing the least significant term at each step on the 2004 dataset. We then tested the 15 best models from the 2004 dataset, plus the global model and all models that did not include interaction terms, on the complete dataset. We did not include interaction terms without main effects. Values are presented as means ± 1 SD.

To examine the effect of bias on estimates of food intake rates, we created 10 groups of 500 feeding observations designed to mimic our actual dataset. We then applied the general linear models developed earlier to simulate actual bias with the associated error terms. We compared three separate quantitative procedures to see how closely they approximated actual data: (1) no correction using average fish size per prey type, (2) correction for number of missed feedings,

and (3) correction for number of missed feedings and misidentification of fish lengths. Energy intake rates were estimated by multiplying energy densities (kJ/g) by mass (in g) determined from mass-length relationships for prey items at Coats Island, using the lengths generated by the simulations (Elliott and Gaston 2008). The mean energy intake value for all identified feedings was used as the value for unidentified feedings (Elliott et al. 2006).

RESULTS

Missed arrivals. Of 889 returns to the colony recorded by the TDRs, 13% were missed by observers. The proportion of missed visits was highest between 20:00 and 04:00 (Fig. 2). The best AIC model with missed visits as the dependent variable included independent terms for time of day, time since the last feeding, time since the start of watch, and distance (Table 1). The best AIC GLM had logit terms of 0.92 ± 0.35 cos/d for time of day ($t_{882} = 2.7$, $P = 0.008$), 0.34 ± 0.14/m for distance to site ($t_{882} = 2.4$, $P = 0.02$), 0.0025 ± 0.0019/min for time since start of watch ($t_{882} = 1.4$, $P = 0.17$), 0.0038 ± 0.0247/min for time since last feeding ($t_{882} = 0.2$, $P = 0.88$), and 0.00011 ± 0.00017 min^{-2} for the interaction between time since start of watch and time since last feeding ($t_{882} = 0.7$, $P = 0.47$). Thus, the proportion of missed visits decreased with light levels (time of day) and increased with distance from the site. Time since the last feeding and since the start of an observation period were less important, but still included in the best AIC model. There was no difference among observers in proportion of missed visits ($F_{11,876} = 0.9$, $P = 0.5$).

Unidentified prey. Of 3744 feedings observed, prey were not identified for 487 (13%) feedings. Although the best AIC model with unidentified prey as the dependent variable included time of day and whether the site was obscured or not, AIC models including distance to site also had low AIC values (Table 1). The best AIC GLM had logit terms of 0.45 ± 0.08 cos/d for time of day ($t_{3741} = 5.7$, $P < 0.0001$) and 0.38 ± 0.11 for whether the site was obscured ($t_{3741} = 3.4$, $P = 0.0008$). Thus, the proportion of unidentified prey increased with decreasing light levels (time of day; Fig. 2) and for sites that were obscured. The proportion of unidentified prey may have also increased with distance to the
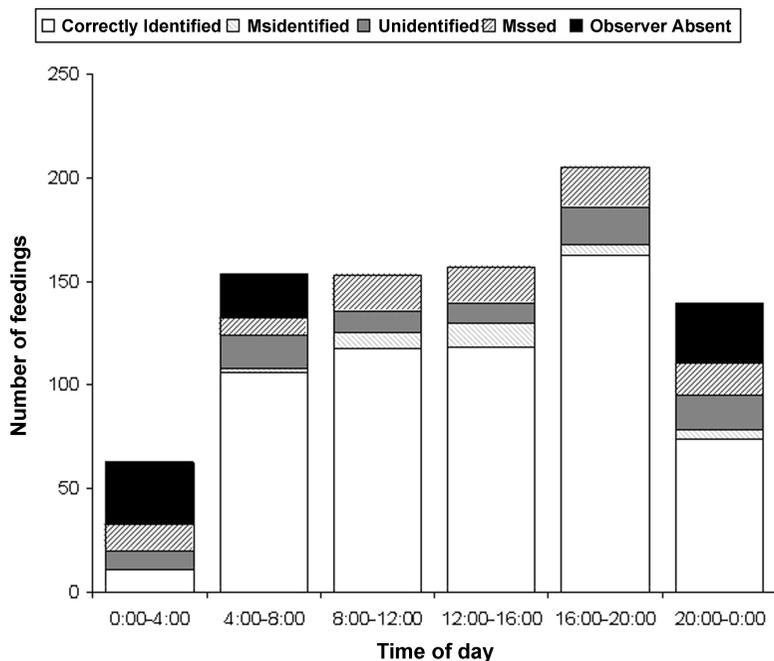
Fig. 2. The percentage of incorrectly identified Thick-billed Murre prey at Coats Island, Canada, increased during periods with low light level ($N = 889$ total observations by recorder). The category for "Observer Absent" represents feedings missed because no observer was present. The values for misidentified prey were extrapolated from the subset ($N = 226$) of specialist prey items where prey type could be assigned from recorder profiles.

site because AIC models including distance to site had low AIC values. There was a difference in the proportion of unidentified prey among observers ($F_{12,3747} = 4.9$, $P = 0.0005$), but this was largely due to more unidentified prey by one observer.

Misidentified prey. Of 226 prey identified using TDR recordings (and excluding generalist

Table 1. Ranking of logistic models describing whether (1) feedings were missed or not, (2) prey were unidentified or not, and (3) prey were misidentified or not during feeding observations of Thick-billed Murres at Coats Island, Canada ($N = 3744$). ΔAIC values for models with ΔAIC < 2 are shown. AIC rankings are only relevant within each column.

| Model	Missed		Unidentified		Misidentified	
	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight
Time of day + obscured			0.0	0.48	0.0	0.30
Time of day + obscured + time×obscured + distance			1.5	0.23		
Time of day + time since last feed + time since start of watch + (time since last feed) × (time since start of watch) + distance	0.0	0.46				
Obscured					0.5	0.24
Time of day + obscured + distance					1.4	0.15
Global	7.7	0.02	8.1	0.01	8.1	0.01
Null	13.3	0.00	41.6	0.00	3.4	0.06
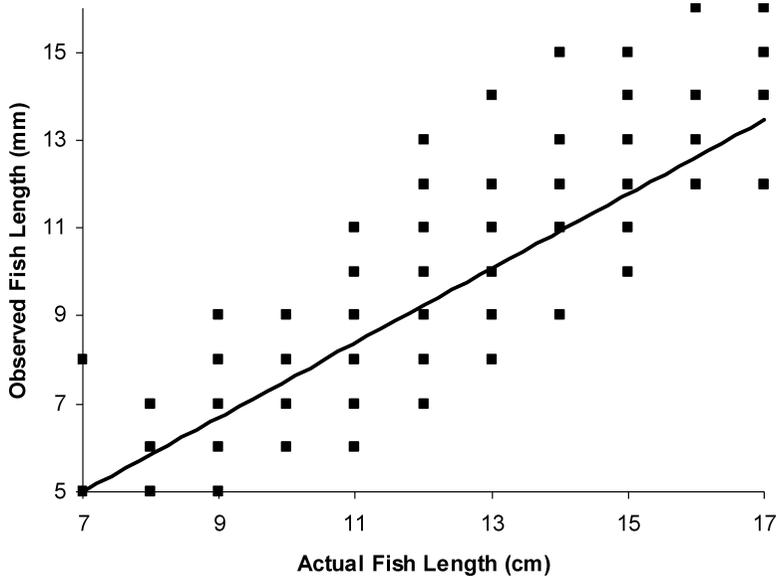
Fig. 3. Observed fish length (mm) for Thick-billed Murre feeds at Coats Island, Nunavut 2004–2007 was lower than actual fish lengths (mm). Note that many points represent multiple values. Regression: Observed Fish Length = 1.04 Actual Fish Length + 1.94 ($R^2 = 0.71$).

prey), 5% were considered misidentified because the TDR trace was unusual for that prey item. The best AIC logistic model with misidentified prey as the dependent variable included time of day and whether the site was obscured or not (Table 1). The best AIC GLM had logit terms of –0.88 ± 0.57 cos/d for time of day ($t_{222} = 1.5$, $P = 0.12$) and 1.83 ± 1.06 for whether the site was obscured or not ($t_{222} = 1.7$, $P = 0.08$). Thus, the proportion of misidentified prey increased with light levels (time of day) and when the site was obscured. Nonetheless, there was little support for any model above the null model ($\Delta AIC = 3.4$) and these conclusions must be viewed with caution. The proportion of misidentified prey was highest between 8:00 and 16:00 (Fig. 2), but sample sizes were small between 23:00 and 4:00 (only four feedings). Observers did not differ in the proportion of misidentified prey ($F_{8,213} = 0.6$, $P = 0.77$). Fish lengths were consistently about 2 cm longer than estimated by observers (Fig. 3).

Energy intake estimates. For the simulations and based on our results, we removed 13% of the feeding visits and labeled 13% of prey as unidentified and 5% as misidentified, with error distributed randomly within the 95% confidence intervals outlined for the effects described by the general linear models. In the simulated

dataset, chicks averaged 112 ± 8 kJ/d. We estimated that chicks averaged 56 ± 1 kJ/d without corrections, and 64 ± 2 kJ/d once corrected for missed feeds. After correcting for fish length, we estimated that chicks received 110 ± 4 kJ/d.

DISCUSSION

During our observations, 13% of all feeding visits were missed and, of those recorded, 13% of the prey items were unidentified and 5% misidentified. More feedings were missed and more prey unidentified when light levels were low, and more prey were misidentified during midday, possibly because higher food delivery rates meant that less attention was paid for each prey item. The proportion of unidentified prey was also influenced by time of day and site location, with more prey recorded as unidentified at sites that were partially obscured or distant from the observer. Bias associated from unidentified prey can be corrected for if one assumes that the distribution of prey types and lengths is similar between identified and unidentified prey. Similarly, Cézilly and Wallace (1988) and Gonzales-Solis et al. (1997) found that visual observations resulted in many misidentifications for small items, but were reliable for larger items.

Observers tended to underestimate fish lengths by about 2 cm, presumably because either more of the fish was inside of the bird's bill than believed or because tail fins that tend to be clear were missed and not included in the estimate. Gaston and Nettleship (1981) also found that fish lengths estimated by observers during Murre feeding watches were significantly lower than those found on ledges or collected from chicks fitted with ligatures. Because we found a strong relationship between observed and actual fish length, robust estimates of actual fish lengths could be obtained by adding a correction factor of 2 cm.

The importance of particular sources of bias depends on the questions asked. For example, measures of dietary trends over time (e.g., Gaston et al. 2003) are unlikely to be affected by time of day biases, provided that prey composition is unaffected by time of day biases or that observations are always made at the same time of day. On the other hand, estimates of prey intake could be underestimated. Indeed, we found that feeding rates and fish lengths and, therefore, energy intake rates were underestimated by 50%, perhaps explaining why previous researchers suggested that energy intake by chicks at Murre colonies was low compared to estimates of the energy required to sustain observed growth rates (Gaston 1985, Birkhead and Nettleship 1987, Hipfner et al. 2006). Furthermore, male and female Thick-billed Murres forage at different times of the day (Jones et al. 2002), and bias due to time of day could affect intersexual comparisons of feeding rates and related parameters (Paredes et al. 2006). Because previous studies of Murre feeding rates, energy intake rates, and prey composition included observations during midday and periods of low light (when misidentification rates were highest in our study) and at greater distances between blinds and the birds than in our study (up to 100 m distance; Birkhead and Nettleship 1987, Hatchwell 1991, Harris and Wanless 1993, Uttley et al. 1994, Bryant et al. 1999, Zador and Piatt 1999, Davoren et al. 2003, Gaston et al. 2003, Hipfner et al. 2006, Lewis et al. 2006, Paredes et al. 2006, Cameron-MacMillan et al. 2007, Harding et al. 2007, Doody et al. 2008, Elliott et al. 2008a,b), the biases reported in our study likely also influenced the results reported in those studies.

To conclude, we found many sources of bias in our observations that translated into a systematic underestimation of energy delivery rates. Although some biases may be limited to our study site or to studies of Murres, others may be common among avian feeding studies. For example, where visual observations have been compared to video observations, the proportion of unidentified food items (18%, Margalida et al. 2005) and missed feedings (33%, Elliott et al. 2005; "considerable," Harris 1984; no difference in feeding rate between videos and visual observations, Warnke et al. 2002; higher feeding rate for videos than visual observations, Harding et al. 2007) is usually considerable. We know of no other study that has examined the effect of time of day, but time of day biases may be a problem in many studies because feeding rates are generally highest early in the morning (e.g., Hutto 1981, Elliott et al. 2005, 2006) and many research questions rely on accurate measures of actual feeding rates or how feeding rates change with time of day or location. We recommend that investigators carefully plan studies of provisioning behavior by choosing times of day, locations, and watch durations that minimize potential bias. Even with well-planned studies, more information is needed on possible biases associated with feeding rates and related parameters across a wide variety of birds. Using correction factors derived from information collected from a subset of observations measured independently (TDRs, double survey, or videocameras), unbiased estimates of feeding rates are possible. We recommend that researchers carefully plan studies to minimize bias, attempt to measure bias on a subset of their data, and consider the possible impact of bias on the questions being asked.

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