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Use of time-activity budgets to measure early progress of a social attraction restoration project

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ABSTRACT

Social attraction is a useful technique for re-establishing or relocating waterbird colonies and other species groups. However, little information exists regarding how newly attending individuals behave when the social environment is influenced predominantly by artificial stimuli. To help assess early progress of colony re-establishment, we compared time-activity budgets of common murre (*Uria aalge*) at a social attraction site (Devil's Slide Rock; DSR) in central California with two nearby reference colonies during the first 3 years (1996–1998) of efforts. Murre at all colonies spent over 95% of their time engaged in resting, comfort, courtship, and alert activities during the pre-breeding period and over 88% of their time in similar activities during the breeding period. Although patterns were similar overall, comparisons of pooled and year-specific time budget data revealed significant differences between all three colonies, especially during pre-breeding. Murre at DSR typically engaged in comfort behaviors less frequently and in alert and courtship behaviors more frequently than reference colonies. Differences likely were due to recent re-establishment, including lower bird densities and higher proportions of non-breeders and first-time breeders at DSR, along with other factors such as disturbance. Results indicate that newly attracted birds at DSR behaved “normally” even though the social environment was influenced predominantly by artificial stimuli. Furthermore, re-established breeding in the first year of efforts, subsequent colony growth, and high productivity reflected successful restoration efforts. Thus, time-activity budgets can provide important measures of early progress of social attraction efforts and as such can be used to inform adaptive management decisions.

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1. Introduction

Conservation and restoration of animal populations has traditionally focused on identifying and managing for environmental threats such as habitat destruction, reduced reproduction, or heightened mortality. However, conservationists have begun to recognize that understanding an animal's behavior may be just as

important for conservation and restoration efforts as understanding and managing its external environment (Caro, 1999; Sutherland, 1998) and have begun developing conservation techniques that take behavior into account. “Social attraction” is one such technique. Originally developed from work on conspecific attraction in colonial breeding birds (Lack, 1966), social attraction uses social stimuli, typically consisting of decoys, playbacks of recorded vocalizations, and/or mirrors to mimic the visual and auditory cues of conspecifics to influence the recruitment of potential breeders (Kress, 1983) and induce breeding behaviors (O'Connell-Rodwell et al., 2004; Pickering and Duverge, 1992). Multiple studies have demonstrated that social attraction influences both colonial (Jeffries and Brunton, 2001; Kress, 1983; Podolsky and Kress, 1992; Roby et al., 2002) and non-colonial birds (Ahlering et al., 2006; Hahn and Silverman, 2007; Harrison et al., 2009; Ward and Schlossberg, 2004). The description of conspecific attraction in mammals (Hoek, 1989; Weddell, 1991) and reptiles (Stamps, 1991) suggests this technique may have wider conservation applications.

Abbreviations: CR, Castle Rocks and Mainland; DSR, Devil's Slide Rock; PR, Point Reyes; USFWS, United States Fish and Wildlife Service.

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Social attraction has been used successfully to re-establish or relocate colonies of various colonial breeding birds (Kotliar and Burger, 1984; Kress, 1997, 1998; Parker et al., 2007; Roby et al., 2002), yet little information has been obtained regarding the behavior of newly attending individuals in response to social attraction equipment or other factors associated with newly (re-) established colonies. It often takes several years after birds are first attracted to a desired location before breeding actually occurs (see Kotliar and Burger, 1984; Kress, 1983; Kress and Nettleship, 1988), especially for species that are long-lived or take time to reach a critical number or density. When conducting social attraction or other restoration techniques, progress or success is often evaluated by how many breeding individuals recruit to the site. However, in cases where initiation of breeding is delayed or limited, conservationists and managers are faced with the challenge of assessing the progress of restoration efforts in the absence of any actual breeding and other methods of evaluation are necessary to assist adaptive management decisions. In addition to examining numerical and temporal patterns of attendance, another way to determine early progress of colony re-establishment is to evaluate whether newly attending individuals engage in normal behaviors that: (a) should eventually result in the establishment of breeding (e.g. mating displays, courtship activities, etc.); or (b) if initial breeding occurs rapidly, normal behaviors suggest that continued successful breeding and colony growth can be expected. If newly attending individuals immediately breed or show behavior patterns indicative of future breeding, continuation of similar social attraction applications can be expected to have a greater likelihood of future success, partly justifying continued cost and effort. However, if primarily non-breeding or abnormal behaviors are observed, future breeding may be less likely and project modification should be considered.

On the central California coast, a breeding colony of nearly 3000 common murres (*Uria aalge*; hereafter, “murres”) at Devil’s Slide Rock (DSR) was extirpated (i.e. no further breeding) in 1986 because of high mortality in a local gill-net fishery, high mortality from the January 1986 *Apex Houston* oil spill, and other factors (Carter et al., 2001, 2003; Takekawa et al., 1990). Between 1986 and 1994, small numbers of murres attended DSR sporadically but breeding was unlikely (Carter et al., 2001, 2003; Parker et al., 2007). Because murres breed colonially and have high colony philopatry, mate and breeding site fidelity (Gaston and Jones, 1998; Halley et al., 1995; Harris et al., 1996), they typically return to breed at their natal colonies or occasionally join existing colonies. As a result, they rarely re-establish extirpated or abandoned colonies and often take decades or more to do so (Carter, 2004; Carter et al., 2001; Manuwal and Carter, 2001). Social attraction can speed colony re-establishment and subsequent growth by encouraging birds to attend abandoned habitats more rapidly, in larger numbers, and induce breeding behaviors. Starting in 1996 with *Apex Houston* oil spill settlement funds, social attraction was employed to re-establish the colony at DSR (Parker et al., 2007).

We compared time-activity budgets of murres at DSR with two nearby established reference colonies. The initial intent of gathering time-activity budget data was to provide information on the progress of restoration prior to re-establishment of breeding, which was expected to take several years. However, since breeding was re-established in the first year that social attraction equipment was deployed (Fig. 1; Parker et al., 2007), time-activity budgets were examined only during the first 3 years of social attraction efforts and colony re-establishment (1996–1998). Murre behavior on DSR was influenced by small numbers of actively breeding birds in all 3 years of the study, but the majority of attending birds were not actively breeding and social attraction equipment well outnumbered attending birds. Thus, social attraction equipment provided the bulk of social stimuli. We expected that if social attraction successfully mimicked the social stimuli of an estab-

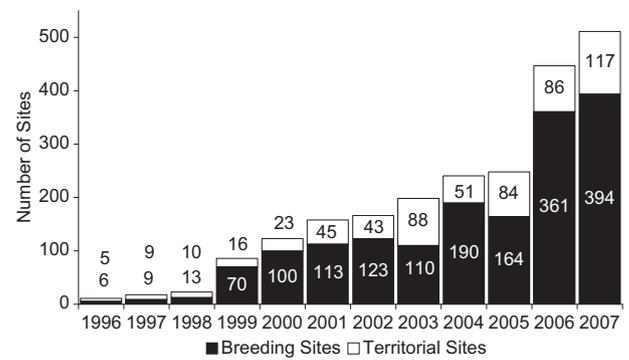


Fig. 1. Number of Common Murre breeding and territorial sites at Devil’s Slide Rock, 1996–2007. Numbers within or above bars indicate sample sizes.

lished colony, then murres attracted to DSR would display normal behavioral patterns and time-activity budgets would not be significantly different from reference colonies.

2. Materials and methods

2.1. Study colonies

We conducted observations of murre time-activity budgets at three colonies along the central California coast from 1996 to 1998, including the DSR restoration site and two reference colonies for comparison. Social attraction was employed to re-establish breeding at DSR (37°34’N, 122°31’W), a small sea stack (22 m high) located approximately 300 m from the mainland shore. The top of DSR consists of about 200 m² of relatively flat vegetation-free substrate and supported 12–26 breeding murres (6–13 pairs) in 1996–1998 (Fig. 1; Parker et al., 2007).

Point Reyes (hereafter, “PR”; 37°59’N, 123°59’W), within Point Reyes National Seashore, is the largest (ca. 27,000 breeding birds) colony in the study and is 63 km northwest of DSR. PR is comprised of multiple subcolonies scattered along much of the Point Reyes Headlands (Carter et al., 1992). We conducted observations at several subcolonies but report results only from the largest subcolony, Lighthouse Rock, where studies on reproductive performance also were conducted. Lighthouse Rock is fairly large and devoid of vegetation, approximately 20 m high and 10 m from the mainland and supported about 18,000 breeding birds in 1996–1998 (USFWS, unpublished data).

Castle Rocks and Mainland (hereafter, “CR”; 36°22’N, 121°54’W) is located 144 km southeast of DSR and is comprised of numerous subcolonies on mostly un-vegetated sea stacks and cliffs. We conducted observations at several subcolonies but report results only from subcolony CR4, where studies on reproductive performance also were conducted. CR4 is a sea stack about 20 m high and 300 m from the mainland and supported approximately 1000 breeding murres in 1996–1998 (USFWS, unpublished data). Both DSR and CR are now part of the California Coastal National Monument, managed by the US Bureau of Land Management.

2.2. Social attraction design

On 12–13 January 1996, 384 life-sized adult murre decoys were deployed on DSR along with twelve 3-sided mirror boxes and two independent audio systems (compact disc player, amplifier, and speakers). To further simulate active breeding, 48 egg and 36 chick decoys were added on 14 April 1996 (see Parker et al., 2007 for more details). Except for the photovoltaic panels and speakers, social attraction equipment was removed each year after all breeding

and attendance had ceased for the season. Decoys were cleaned, repaired, and repainted, then were redeployed along with audio equipment on 30–31 January 1997 (with egg and chick decoys on 26 March 1997) and 5–6 March 1998 (with egg and chick decoys on 20 March 1998). Social attraction equipment was not used at either CR or PR.

2.3. Time-activity budgets

Time-activity budget data were collected at all three colonies for the first 3 years of the DSR restoration project; thereafter, murre colony status continued to be measured by changes in colony size and reproductive performance. Data collection occurred from 2 February to 27 July 1996, 6 January to 23 July 1997, and 13 January to 4 August 1998. Scan-sampling techniques (Altmann, 1974) were used at each colony to quantify the proportion of time murre spent in different activities. Protocols were adapted for differences in colony size, seasonal variation in murre attendance, and logistical limitations. At DSR, morning and afternoon watches were performed 4–6 times per week. Morning watches began when lighting was adequate to observe birds through spotting scopes (ca. 30 min after sunrise) and lasted 3–4 h. Afternoon watches lasted 3 h and cycled through watches beginning at 4.5, 6.5, 8.5, and 10.5 h after sunrise, such that all daylight hours were observed every 4 observation days. As a point of reference, the estimated times of sunrise for San Francisco, California, USA, were 0613 h, 0548 h, and 0658 h PST for the vernal equinox (21 March), summer solstice (20 June), and autumnal solstice (22 September), respectively.

At CR and PR, from 1 January to 15 March, time-activity surveys were performed from 0800 to 1100 h on alternating days throughout each week. From 15 March to 15 May, two 3-h surveys were conducted every 3 days, such that one survey began 30 min after sunrise and the other surveys cycled through the time of day until all daylight hours were sampled each week. From 15 May to 4 August, 3-h surveys were conducted every other day, alternating start times such that all daylight hours were sampled each week.

During each time-activity survey, an activity scan was conducted every 10 min. At DSR, the activity of every bird present was recorded on each scan, up to a maximum of 60 birds. At CR and PR, the behavior of every fifth bird along a transect line was recorded at the instance of observation until a total of 30 (1996), 60 (1997–1998), or all birds present, whichever came first, had been recorded. If fewer than 30 or 60 birds were observed on a given transect, a new transect was selected and data collection continued on the new transect until the activities of 30 or 60 birds, respectively, had been recorded. Activities were dictated on a tape recorder and later transcribed. All observations were performed from standardized locations using Questar telescopes with either a 16 mm (105×) or 24 mm (65×) eyepiece, depending on the distance to the colony.

Murres engaged in 31 defined activities (adapted from Ainley et al., 2002; Birkhead, 1978; Gaston and Jones, 1998) that we grouped into 8 general categories for analyses (Table 1). Excluded from DSR analyses were: (a) activities of murres hidden by social attraction equipment or rocks recorded as “unknown behavior” (0.9% of the total observations); and (b) activities of murres categorized as interacting with social attraction equipment (<0.01% of total observations). We divided observations into “pre-breeding” and “breeding” periods. The pre-breeding period was defined as starting on 1 January and ending on the median egg lay date for first eggs for a given colony in a given year. Median egg lay date was used because before this date over half of the breeding population did not have eggs yet and a substantial proportion might still be engaging in non-breeding behaviors. The breeding period was defined as beginning the day after the median first egg lay date and ending on the median chick departure date. Median chick departure date was used as the ending date because a high proportion of birds present after that date were not attending eggs or chicks and thus were post-breeding or non-breeding birds. Because murres stopped attending the colonies at or soon after the last chick departed, small sample sizes prohibited comparisons of post-breeding behavior.

2.4. Statistical analysis

We examined variation in time-activity budgets of murres between colonies by using separate generalized linear models (GLMs) to analyze the proportion of time spent in each of the eight activity categories (eight models per period). To reduce the influence of individual birds, we excluded scans when activities of less than six birds were recorded. To make general comparisons between colonies, we pooled data across years and constructed models for pre-breeding and breeding periods for a total of 16 models (2 periods × 8 categories). To examine year-specific differences between colonies, we repeated the analyses separately by year, for a total of 48 models.

For each GLM and its corresponding activity category, we treated each scan as an independent binomial observation consisting of the number of birds engaged in that activity and for seven other activities combined, and designated colony as a categorical predictor variable (Agresti, 2002; Venables and Ripley, 2002). Models based on a binomial distribution with a logit-link showed signs of overdispersion (deviance/df > 100; Agresti, 2002). Therefore, we constructed models using the quasi-binomial method with a logit-link which adjusted for the overdispersion and had a better goodness of fit (deviance/df < 1.10; Agresti, 2002). Because the budget of each activity is negatively related to other activities, comparisons among the three colonies are not independent across the eight behaviors and Bonferroni-corrected *p*-values ($k = 24$; Bonferroni-corrected significance level = $0.05/24 = 0.002$) are presented. All statistical analyses were performed using the statistical package R (R Development Core Team, 2009); Tukey multiple

Table 1
Common murre time-activity budget categories recorded at colonies in central California.

Activity categories	Number of field activities	Activities descriptions
Agonistic	3	Jabbing, aggressive interaction with cormorant or gull
Alert	2	Standing with neck extended looking around, head-bobbing, wing flapping associated with head-bobbing
Breeding	5	Incubating, brooding, allo-preen mate or chick, attending neighbors chick, feeding chick
Comfort	5	Head scratch, head shake, preening, stretching, wing flapping not associated with head-bobbing
Courtship	9	Allo-preening, bill fencing, copulation, copulation attempt, fish presentation to mate, ground-inspection, parading, pebble presentation, sky-pointing
Locomotion	2	Flying, walking (birds landing/taking off were recorded as flying)
Rest	3	Sleeping, sitting or standing at rest
Other	2	Other behaviors (not included in above categories)

comparison tests were performed using the “multcomp” add-on package (Hothorn et al., 2008). Observation effort and therefore sample sizes differed between colonies due to logistical constraints and weather; data from subcolonies lacking reproductive performance information also were excluded from analyses.

3. Results

We used data from 12,123 behavioral scans totaling 1564 observation hours over 459 days: 7533 scans (947 h) over 242 days at DSR; 1486 scans (191 h) over 80 days at PR; and 3104 scans (426 h) over 137 days at CR (Table 2). Pooling each colony’s data over 3 years, we constructed average time-activity budgets for each colony. During the pre-breeding period, resting, comfort, alert, and courtship behaviors accounted for over 95% of time-activity budgets (Fig. 2), with the largest proportion consisting of resting-related activities (range: 47–54%). At CR and PR, comfort, alert, and courtship activities were successively next most frequent. However, at DSR, alert and comfort behaviors were next most frequent followed by courtship. Combined agonistic, breeding, locomotion, and “other” behaviors accounted for less than 5% of murre time-activity budgets at all colonies.

During the breeding period, resting, breeding, alert, and comfort activities were most prevalent, accounting for over 88% of time-activity budgets (Fig. 2). At DSR and PR, resting and breeding activities were most prevalent, followed by alert and comfort activities at DSR and comfort and alert activities at PR. At CR, resting activities were followed by comfort, breeding, and alert activities.

Significant differences in pooled time-activity budgets occurred between colonies during the pre-breeding and breeding periods (Fig. 2). During pre-breeding, birds at DSR spent more time engaged in courtship activities (all $p < 0.001$) and less time in comfort activities (all $p < 0.001$) than at reference colonies. Comfort was the only category that differed significantly between all three colonies. Significant differences between CR and PR also occurred in the rest category. Fewer differences between colonies occurred during breeding. Time-activity budgets differed significantly between CR and DSR in alert behaviors ($p < 0.001$) and CR differed from both DSR and PR in comfort behaviors (both $p < 0.001$).

In inter-annual comparisons, greater numbers of significant differences in the time-activity budgets occurred between colonies during pre-breeding ($n = 14$; Table 3) than breeding ($n = 3$; Table 4). During pre-breeding, DSR differed significantly from both reference colonies in three comparisons: alert 1997, comfort 1998, and courtship 1998. In contrast, CR differed from both DSR and PR in one comparison (comfort 1997), while PR never differed from the other colonies. Other differences were between DSR and CR

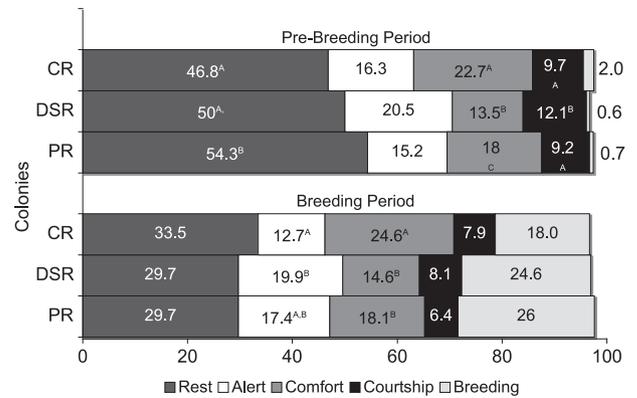


Fig. 2. Average percentage of time common murre spent in the top five activity categories at Castle Rocks and Mainland (CR), Devil’s Slide Rock (DSR), and Point Reyes (PR) during the pre-breeding and breeding periods, using data pooled throughout 1996–1998. Values with different superscripts within an activity category and period were significantly different. p -Values for pairwise comparisons between colonies were corrected using the Bonferroni method for multiple comparisons ($k = 24$; p -value of 0.05 = 0.002).

(comfort 1996, locomotion 1996, and courtship 1997), DSR and PR (rest 1997 and agonistic 1997) and CR and PR (agonistic 1998).

The only significant differences found during breeding were that CR differed from both DSR and PR in comfort activities in 1997 and from PR in alert activities in 1998. Murres at DSR consistently spent the least while those at CR spent the most time in comfort behaviors (Fig. 2, Tables 3 and 4). To further explore frequent differences between CR and DSR in the comfort category (four significant tests between pre-breeding and breeding periods), we examined the field behaviors that comprised this category and found that CR and PR were similar in that “head shake” and “wing flap” behaviors each accounted for 25% of this category, respectively, with preening responsible for the remaining 50%. At DSR, preening comprised 82% of this category while “head shake” and “wing flap” accounted for only 12% and 6%, respectively. Despite a lack of significant differences, murres at DSR also spent more time in courtship (especially during the pre-breeding period) and alert behaviors (except for 1998) than at the reference colonies.

During the strong 1998 El Niño event, murres at DSR spent considerably less time displaying comfort behaviors and a significantly higher proportion of time engaged in courtship activities during pre-breeding than either CR ($p = 0.001$) or PR ($p = 0.001$). Murres at DSR also spent more time engaged in courtship activities during the 1998 breeding period (DSR vs. CR: $p = 0.01$ and DSR vs. PR: $p = 0.01$); however, these differences were not significant after Bonferroni correction.

Table 2

Number of observation days, hours, and scans for common murre time-activity budget surveys at three central California colonies, 1996–1998.^a

Colony		1996		1997		1998		Total	
		Pre	Breed	Pre	Breed	Pre	Breed	Pre	Breed
DSR	Days	60	43	64	30	33	12	157	85
	Hours	261	151	230	145	122	38	613	334
	Scans	2460	1941	1262	928	733	209	4455	3078
PR	Days	18	3	17	7	30	5	65	15
	Hours	38	9	33	23	73	15	144	47
	Scans	452	97	253	144	451	89	1156	330
CR	Days	22	11	17	20	35	32	74	63
	Hours	50	29	45	65	125	112	220	206
	Scans	600	339	275	411	801	678	1676	1428
Total	Days	100	57	98	57	98	49	296	163
	Hours	349	189	308	233	320	165	977	587
	Scans	3512	2377	1790	1483	1985	976	7287	4836

^a Abbreviations: DSR (Devil’s Slide Rock); PR (Point Reyes); CR (Castle Rocks and Mainland); Pre (Pre-breeding period); Breed (Breeding period).

Table 3
Average percentage of time common murres spent in eight activity categories at three central coastal California colonies during the pre-breeding period, using data for each year from 1996 to 1998. *p*-Values for pairwise comparisons between colonies were corrected using the Bonferroni method for multiple comparisons ($k = 24$; p -value of 0.05 = 0.002). Values with different superscripts within an activity category and period were significantly different.^a

Activity category	1996			1997			1998		
	DSR	PR	CR	DSR	PR	CR	DSR	PR	CR
Rest	51.8	59.0	55.0	43.9 ^A	55.5 ^B	45.1 ^{A,B}	54.2	50.4	44.2
Alert	21.4	16.2	14.7	26.4 ^A	15.9 ^B	16.0 ^B	12.7	14.1	16.9
Comfort	11.4 ^A	13.9 ^{A,B}	17.2 ^B	14.3 ^A	17.0 ^A	26.8 ^B	15.5 ^A	21.7 ^B	23.4 ^B
Courtship	11.4	9.1	11.2	11.6 ^A	9.0 ^{A,B}	8.3 ^B	13.6 ^A	9.3 ^B	9.6 ^B
Breeding	0.8	0.01	0.4	0.2	0.5	0.5	0.9	1.1	3.1
Locomotion	2.4 ^A	1.0 ^{A,B}	0.8 ^B	2.1	1.0	2.1	2.2	2.2	1.9
Agonistic	0.6	0.4	0.5	1.0 ^A	0.4 ^B	0.9 ^{A,B}	0.5 ^{A,B}	0.7 ^B	0.3 ^A
Other	0.2	0.4	0.2	0.5	0.6	0.4	0.4	0.6	0.5

^a Abbreviations: DSR (Devil's Slide Rock); PR (Point Reyes); CR (Castle Rocks and Mainland).

Table 4
Average percentage of time common murres spent in eight activity categories at three central coastal California colonies during the breeding period, using data for each year from 1996 to 1998. *p*-Values for pairwise comparisons between colonies were corrected using the Bonferroni method for multiple comparisons ($k = 24$; p -value of 0.05 = 0.002). Values with different superscripts within an activity category and period were significantly different.^a

Activity categories	1996			1997			1998		
	DSR	PR	CR	DSR	PR	CR	DSR	PR	CR
Rest	30.4	20.1	33.3	29.4	30.2	24.3	27.5	34.2	39.1
Alert	21.4	18.1	10.8	19.5	12.7	15.5	15.8 ^{A,B}	24.8 ^B	11.5 ^A
Comfort	12.0	13.1	13.7	16.8 ^A	16.5 ^A	26.4 ^B	18.9	23.4	26.2
Courtship	7.8	6.3	6.9	6.4	6.4	7.3	13.0	6.3	8.5
Breeding	25.7	40.5	33.8	24.5	32.4	22.0	21.0	7.4	11.7
Locomotion	2.0	1.3	1.0	2.5	1.2	3.4	3.0	2.7	1.7
Agonistic	0.6	0.6	0.5	0.8	0.5	0.9	0.6	0.8	0.5
Other	0.1	0.03	0.1	0.2	0.3	0.2	0.2	0.4	0.8

^a Abbreviations: DSR (Devil's Slide Rock); PR (Point Reyes); CR (Castle Rocks and Mainland).

4. Discussion

During the pre-breeding period, over 95% of murre time-activity budgets at all three colonies were comprised of resting, comfort, courtship, and alert activities. In the breeding period, resting, breeding, alert, and comfort activities accounted for over 88% of time-activity budgets at all three colonies. Thus, murres at DSR apportioned their time in a similar manner to murres at the reference colonies. Given that (a) murres began breeding in the first year social attraction equipment was deployed on DSR (1996) after a decade without breeding, (b) over 90% of all murres were recorded in decoy vs. control plots, and (c) 5 of 6 nests in 1996 were located within 60 cm of mirror boxes, it is clear that social attraction equipment was involved in attracting murres to DSR through successful mimicking of social cues that assisted initiation of breeding (Parker et al., 2007). Even if some newly attending individuals did not immediately engage in overt breeding behaviors, time-activity budgets revealed behavior patterns indicative of potential future breeding (e.g. courtship displays, copulation attempts) at DSR, suggesting continued efforts to re-establish the colony were likely to be successful. Productivity (number of chicks fledged per breeding pair) at DSR in 1996–2002 also was comparable to if not higher than reference colonies (mean chicks/pair: DSR = 0.76; CR = 0.58; PR = 0.60; USFWS, unpublished data) and the colony grew slowly between 1996 and 1998, then more rapidly from 1998 to 2005 (Fig. 1). Early progress of colony re-establishment in 1996–1998 was encouraging to continue restoration efforts for several more years. In 2000, DSR reached the initial 10-year goal of 100 breeding pairs. Social attraction efforts were discontinued following the 2005 breeding season because of high colony productivity and continued growth. As of 2007, there were 394 breeding pairs and another 117 territorial sites. In retrospect, time-activity budgets combined with other data were good early

indicators of later colony growth that was encouraged by social attraction equipment.

While murres at the three colonies apportioned their time similarly, closer inspection of time-activity budgets did reveal some differences between colonies. However, differences between the reference colonies were generally similar in magnitude to differences between reference colonies and DSR. In general, differences seemed to reflect natural variation or human-related factors (i.e. disturbance) between colonies.

Less time in comfort activities at DSR was likely due mainly to factors associated with recent colony re-establishment. Although immediate breeding in 1996 suggested some survivors from the former DSR colony returned, most attending murres at DSR in 1996–1998 (especially during pre-breeding) were likely prospecting immature or adult birds that had hatched at nearby colonies (Parker et al., 2007). In contrast, most birds at reference colonies were established breeders. Prospecting birds likely spend more time engaged in courtship and site acquisition behaviors and less time in comfort behaviors than established breeders, which could account for the elevated courtship and reduced comfort behaviors at DSR (Fig. 2, Tables 3 and 4). Murres also frequently use comfort activities such as preening, stretching, and wing-flapping as appeasement displays to stop or prevent agonistic interactions with conspecifics and these behaviors increase with nesting density (Birkhead, 1978), consistent with established breeders in higher nesting densities at CR and PR in this study.

More time engaged in alert behaviors (often used in response to disturbances; Birkhead, 1978) by murres at DSR (especially pre-breeding) may have reflected differences in human-caused and natural disturbance levels between DSR and the reference colonies. During at least part of this study, DSR and CR also experienced relatively high frequencies of low-level aircraft overflights (Rojek et al., 2007), many of which elicited alert behaviors such as

head-bobbing and occasionally caused birds to flush. However, murres at DSR flushed less frequently than murres at CR; at DSR, decoys and broadcast vocalizations may have encouraged birds to remain instead of flush (Rojek et al., 2007). If true, this likely benefitted DSR colony restoration. However, such potential behavioral modifications should be taken into consideration when planning social attraction projects, as individuals may fail to respond appropriately to predators or may be attracted to low quality habitats if deployment sites are not selected carefully. Additionally, murres at DSR attended and bred in close association with Brandt's cormorants (*Phalacrocorax penicillatus*) but not at the studied portions of reference colonies. While these species often breed in mixed aggregations, competition for space does occur (Ainley and Boekelheide, 1990; this study) and cormorant-murre interactions sometimes elicited alert behaviors. Many alert behaviors at PR in the 1998 breeding period resulted from frequent disturbances by California sea lions (*Zalophus californianus*), which contributed to complete breeding failure that year (Parker et al., 1999).

During the strong 1998 El Niño event, reduced upwelling and warmer ocean temperatures led to reduced prey availability in the California Current System (Hayward et al., 1999; Lynn et al., 1998) and reduced attendance, breeding propensity, and reproductive success for murres and most other seabirds in central California (Hastings et al., 1998; Jones et al., 2008; Parker et al., 1999). In 1998, birds at DSR spent more time engaged in courtship activities than CR and PR during pre-breeding and breeding (Tables 3 and 4), reflecting more breeding activity at DSR than at the reference colonies. Also in 1998, breeding and territorial sites at PR and CR declined by 40% and 49% from 1997, and birds at only 48–49% of these sites actually laid eggs compared to 82–93% in 1997. However, at DSR the number of active sites increased from 18 to 23 (28%) and birds laid eggs at 57% of these sites compared to only 28% in 1997. Social attraction equipment at DSR provided constant social stimuli which may have: (a) influenced birds attending DSR in 1996–1997 to continue attending the colony and exhibit breeding-related behaviors despite poor breeding conditions; and (b) encouraged additional birds to attend DSR. This may have been critical to the continued success of the restoration project. Instead of abandoning DSR, birds bred successfully and returned in even higher numbers in 1999. However, DSR also is located in a local area that may have had better prey availability during El Niño conditions (Ainley et al., 1996), which also may have encouraged local breeding.

5. Conclusions

Time-activity budgets were an effective way to assess whether or not individuals at the DSR restoration site were engaging in normal behaviors that were likely to lead to successful colony re-establishment, especially when numbers of attending individuals were low and social attraction equipment provided the bulk of the social stimuli.

They allowed us to determine that social attraction equipment successfully mimicked the natural social environment of a murre colony and provided the appropriate social stimuli to attract birds to the site, kept them engaged in social interactions once they arrived, and provided the social cues to initiate courtship, pairing, and breeding. Along with other measures of early progress of colony re-establishment, time-activity budget data suggested that social attraction techniques had been well applied and no major changes were required. However, we could not determine to what degree social attraction vs. active breeding by small numbers of murres was responsible for normal behaviors exhibited at DSR in 1996–1998 but consider that both were involved. Gradual and minor changes to social attraction equipment were later applied

to encourage continued growth of the colony and to slowly remove social attraction equipment without significant impacts to breeding murres.

Collecting time-activity budget data is time and labor intensive but is easily integrated with other monitoring activities. Colony, period and year differences highlight the importance of comparing time-activity budgets at different colonies and times when possible, but even 1 year of data can be useful for a more general assessment. While this study focused on a long-lived colonial seabird, conspecific attraction also has been described in colonial (Jeffries and Brunton, 2001; Kress, 1983; Podolsky and Kress, 1992; Roby et al., 2002) and non-colonial birds (Ahlering et al., 2006; Hahn and Silverman, 2007; Harrison et al., 2009; Ward and Schlossberg, 2004), mammals (Hoeck, 1989; Weddell, 1991), and reptiles (Stamps, 1991), which suggests social attraction techniques may be successful in a wide range of taxa. Thus far, social attraction techniques have been applied primarily to both wild and captive (Pickering and Duverge, 1992) colonial waterbirds but is spreading to other species groups, confirming wider conservation applications. We believe assessment of time-activity budgets provide a measure of early progress of restoration projects employing social attraction techniques and recommend their integration into future efforts targeting species that are easily observed.

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