Behavioral evidence of thermal stress from over-heating in UK breeding gray seals.

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ABSTRACT

Gray seals (*Halichoerus grypus*) in the UK exhibit clear preferences for pupping close to pools of water on inland breeding sites. The reasons for this are unclear as seals are thought to derive all their water requirements from the metabolism of fat. Likewise, the prospect of seals over-heating during the UK's cool, damp autumnal breeding seasons, has seemed unlikely, but has not been previously explored. Here, we provide preliminary behavioral evidence of thermal stress in female gray seals breeding on the island of North Rona, Scotland. Video footage provided measures of proximity to, and the proportion of animals bathing in pools, in relation to meteorological data (temperature, mean sea-level pressure, rainfall, wind speed and direction) on four dates spread through a single breeding season. The proportion of females close to pools increased with pressure (warmer, drier conditions) and decreased on wetter days. In addition, analyses of colony wide patterns of seal dispersion showed that females tended to be closer to pools of water at higher pressures and temperatures and at lower wind-speeds. These results provide the first evidence of thermal stress and behavioral thermoregulation through access to pools of water in a phocid breeding in temperate autumnal conditions.

Key words. Grey seal, *Halichoerus grypus*, behavioral thermoregulation, breeding habitat, North Rona

Recent studies of the effects of fine scale habitat on gray seal (*Halichoerus gryp*us) breeding behavior have revealed that local topography influences individuals' behavior and pupping success. Pomeroy *et al.* (2000) demonstrated that the scale of inter-annual pupping site fidelity depended upon the scale of topographical variation. Within this pattern of inter-annual returns, Twiss *et al.* (2001) demonstrated that females preferred pupping sites with particular topographic characteristics. Proximity to water, either in the form of access to the sea or to pools of water located within the breeding colony was the most important habitat feature. Inter-site differences and seasonal changes in the availability of pools strongly influence the local density and distribution of seals (Twiss *et al.* 2001) and the behavior of females (Twiss *et al.* 2000). Redman *et al.* (in press) demonstrated that temporal changes in the availability of pools within the North Rona colony affect the daily behavior patterns of female gray seals with implications for breeding success. Indeed, Redman *et al.* (in press) illustrated the great lengths to which females will go to gain access to water; risking permanent mother/pup separation (leading to pup death), increasing energetic costs (through locomotion) and increasing the frequency of aggressive interactions with conspecifics (Caudron 1998, Twiss *et al.* 2000). The distances that these females traveled to obtain access to water, and the potential costs of their behavior, suggest that water is of critical importance during lactation. Why then is water so important to breeding gray seals, at least on the North Rona colony?

Two likely possibilities are the maintenance of water balance and thermoregulation. Pinnipeds that fast during their breeding episodes are believed to obtain all their water requirements from the metabolism of fat reserves (Irving *et al.* 1935, Ridgeway 1972, Ortiz *et al.* 1978, Schweigert 1993) and there has been no clinical evidence of dehydration during lactation (Kooyman and Drabek 1968, Reilly *et al.* 1996). However, several otariid species have been observed drinking sea water (which may be associated with the flushing of urea: Gentry 1981), and our own observations (PPP, PR, SDT, SM) suggest that gray seals drink from pools on some breeding colonies.

Pinnipeds spend much of their life foraging in open oceans and exhibit numerous adaptations that enable them to retain heat in this cold environment (Bartholomew 1970). Their generally large and rounded body shapes reduce surface area:volume ratios, while the thick fur coat of otariids and the thick layer of sub-cutaneous blubber in phocids and odobeniids provide effective insulation (Bryden 1964, Bartholomew 1970, Riedman 1990). Arterio-venous anastamoses are found throughout the superficial layers of pinniped skin and in their flippers, which lack the thick insulatory blubber layer, allowing regulation of temperature from these areas of the body (Ronald, McCarter and Selley 1977, Riedman 1990). However, some of these adaptations that help pinnipeds retain heat in the water, such as thick blubber and dense fur, may also promote overheating while on land (Bartholomew 1970, Gentry 1973, Pierotti and Pierotti 1979, Riedman 1990, Renouf 1991). This is especially true during the breeding season because seals accumulate large blubber reserves prior to breeding to sustain them during fasting and lactation. Otariids breeding in tropical, sub-tropical or warm summer temperate climates clearly exhibit behavioural mechanisms associated with the prevention of overheating (Bartholomew and Wilkie 1956, Gentry 1973, McCann 1980, Campagna and Le Boeuf 1988, Riedman 1990, Francis and Boness 1991, Renouf 1991). Conversely, phocids breeding in polar or sub-polar conditions benefit while on land or ice from the adaptations that allow them to minimize heat loss (∅ritsland, Lavigne and Ronald 1978, Pierotti and Pierotti 1979, Lavigne 1980, 1983, Renouf 1991) in situations where they are potentially at risk of stress from cold temperatures. However, few studies have examined the possibility of thermal stress from over-heating in phocids breeding in the cooler temperate regions.

In the UK gray seals breed during the cool wet autumn predominantly on wave-washed offshore islands around the coast of Scotland. Under these conditions it is perhaps not surprising that the concept of overheating has not been seriously considered for this population. In this preliminary study, we examine the behaviour of a small group of female gray seals breeding on one of the largest UK colonies, North Rona, in relation to accurate meteorological data, for evidence of thermal stress.

METHODS

The North Rona breeding colony

North Rona (59^{o}06'N, 05^{o}50'W) is a rocky island lying 75.5 km NNW off Cape Wrath, Scotland. The gray seal breeding season at North Rona extends from late September through to late November. The main breeding assemblage on this island is located on the low lying, northern peninsula of Fianuis. This inland breeding area consists of undulating grassy terrain ranging from approximately 2m to 50m above mean sea level, on a slope increasing from 0^{o} immediately above the access points from the sea to approximately 40^{o} furthest inland (Twiss, unpublished data). These slopes are punctuated by irregularly spaced boulders, rocky outcrops and remnants of old stone walls. Females tend to aggregate around pools (Twiss *et al.* 2000, 2001), and North Rona provides many small pools with locations extending far inland. The resulting distribution of individuals differs significantly from randomly distributions (Twiss, unpublished). Pregnant females select pupping sites and give birth to a single pup. At this colony, females generally remain close to their pups throughout lactation, a period of approximately 18 days, during which they fast (Pomeroy *et al.*, 1994). Towards the end of lactation the female enters oestrus and is mated. She then returns to the sea and the pup is abruptly weaned.

These features make North Rona an ideal site for examining seals' usage of pools during the breeding season. Discrete aggregations of females around pools provide an ideal opportunity to study pool-oriented behavior, as they are too distant from access points to commute to the sea.

Behavioral Study group

The seals monitored by video during the behavioral study were located in the southern part of the Fianuis peninsula, some 150m from the nearest access points to the sea. The study site covered approximately 1165m^2 and contained between 5 and 11 adult females. The site was delimited by distinct physical features (rocks) and contained three pools, each of 5 to 7m^2 area, in its centre. The surrounding substrate was grass. All video footage was obtained from this fixed study site. The video camera (Canon Hi 8 model with x20 optical lens and x2 telephoto connector) was located on a sturdy tripod in a wooden hide 180m from and 32m above the area being recorded. This elevation minimized the area of dead ground and provided a good view of all seals in the shot.

Behavioral analyses

The behavioral observations for this study were made from analyses of video footage recorded at the site described above on four dates (the 4th, 7th, 15th and 22nd of October) during the 1998 breeding season. A total of six continuous hours was recorded for each date. Hi 8 video masters were copied onto VHS format tapes so that they could be viewed using a standard TV and video set for behavioral analyses.

Adult females that were visible in the video frame comprised the focal group. The number and identity of females in the focal group varied during the season, with fewer females early in the season compared to later. It was not possible to identify focal individuals between successive dates, therefore focal individuals on each date were assumed to be different, although it was not possible to confirm this with complete certainty. Due to the necessity to maintain a wide field of view (to encompass local movements away from the central pools) and the relatively low resolution of the images, only coarse behaviors were extracted during the analysis of the video-tapes (such as proximity to pool and shifts in location). Data were recorded using behavioral (scan) sampling (Altmann 1974, Martin and Bateson 1993). The entire focal group (all individuals that were visible) were scanned at 30-min intervals noting (a) the total number of females bathing and (b) the total number of females more than one body length from a pool of water.

General seal dispersion patterns relative to pools of water

As part of ongoing research into gray seal breeding biology at North Rona SDT and PPP have built an extensive and detailed ARC-INFO Geographic Information System (GIS) database for the North Rona colony (Twiss *et al*. 2000, 2001). This GIS contains daily meter-accurate locations of all seals within the southern half of the Fianuis peninsula (an area of 185003 m^2) classified by age and sex. These locations are recorded in the field every morning (at 0900 h BST) during the breeding season using accurate and detailed field maps generated from the GIS. In addition the GIS also contains polygon coverages of land extent and all pools of water (land locked water bodies). Thus, using simple protocols within this GIS, we extracted the full distribution of distances from each breeding female to their nearest pool of water for each date during the 1998 breeding season. These data were then compared against the meteorological data for each date.

Meteorological data

Weather data for North Rona during the 1998 breeding season were provided by the UK Meteorological Office (UKMO) via the British Atmospheric Data Centre (BADC). A UKMO Synoptic weather station is located immediately above the study site, being 273m distance from and 69m above the location recorded in the videos. Data were available at hourly intervals. UKMO data contained the following variables:

Temperature – dry-bulb temperature (^{o}C).

Dew-point temperature - the temperature (^{o}C) to which the air must be cooled to produce saturation with respect to water at its existing atmospheric pressure and humidity.

Mean sea-level pressure (mslp) – measured in mb.

Mean hourly wind speed – measured in knots.

No precipitation data were available from the meteorological station on North Rona, however mean sea level pressure (mslp) records provided a proxy for rainfall, with high pressures equating to drier conditions. This was supported by daily field notes taken on North Rona by SDT during the 1998 season, which provided a coarse categorization for each date as having either no rain, or light or heavy rainfall.

Our specific hypothesis that more seals should be observed bathing and/or closer to pools in warmer, drier or less windy conditions was tested using statistical analyses conducted in SPSS (version 8). All data sets were examined for normality and transformed where appropriate prior to conducting parametric tests. Percentages of seals bathing or away from pools were arc-sine transformed prior to statistical analyses. Bivariate correlations (Pearson's, one-tailed) between the percentages of seals bathing or away from pools and the meteorological parameters were performed using daily mean values for each variable (n = 4). Distributions of seal distances to nearest pools from the GIS data were log-transformed prior to statistical analysis. Weather parameters were compared amongst dates using analyses of variance (ANOVA) with Scheffe's post-hoc multiple comparison tests. Stepwise, multivariate linear regressions were carried out to establish which of the measured weather conditions contributed most significantly to variation in the proportion of seals bathing, the proportion of mothers more than one body length away from the pools, and the distances between seals and their nearest pool of water. These models incorporated temperature, dew-point temperature, mslp, wind-speed, date and time as potential explanatory variables. Rainfall was not included due to the lack of resolution of the classification. Variables were retained at a critical level of P = 0.05. In all statistical tests, sample sizes were computed based on the number of days of observation.

RESULTS

Average weather conditions on the four observation dates

Table 1 presents the descriptive statistics for the meteorological parameters on each of the four study dates. Dry-bulb temperatures were significantly lower on the 15th of October than any other date, the remaining dates showing no significant difference ($F_{3,45}$

= 184, P<0.001). Dew point temperatures were also significantly lower on the 15th compared to all other dates. Dew point temperatures on the 7th were significantly higher than those on either the 4th or 15th (15th << 4th < 22nd < 7th, $F_{3,45}$ = 158, P<0.001). Mean sea level pressures (mslp) were significantly different on all sampling dates (22nd << 15th < 4th < 7th, $F_{3,45}$ = 4809, P<0.001). Wind Speeds varied significantly across dates ($F_{3,45}$ = 343, P<0.001) being greater on the 22nd than any other date. The 7th had significantly lower wind speeds than the 4th or 22nd. In addition, the wind direction differed between dates (4th = easterly, 7th = southerly, 15th = northwest, 22nd = southwest). Rainfall was heaviest on the 22nd, light on the 4th and 15th, and the 7th was dry. In summary, the 4th of October was warm with light rain and moderate breezes, the 7th was similarly warm but was dry and calm. The 15th was the coldest with light rain and moderate breezes. The wettest and windiest day was the 22nd, although it was relatively warm.

Seal Behavior from the video-analysis

The proportion of seals bathing exhibited no significant correlations with any of the meteorological parameters. However, bearing in mind the small sample sizes (n = 4), the following trends were suggested: an increase in the proportion of bathing seals with increasing mslp (r = 0.85, n = 4, P = 0.074), and a decrease in the proportion bathing with increasing rainfall (r = -0.82, n = 4, P = 0.091). The proportion of females more than one body length away from a pool of water was significantly correlated with mslp (r = -0.93, n = 4, P = 0.037, Fig. 1) and rainfall (r = 0.98, n = 4, P = 0.011, Fig. 2), such that more seals were away from pools in wetter conditions. No other significant correlations were found, but the following trend was observed: an increase in the proportion of seals away from pools with increasing wind speed (*r* = 0.83, *n* = 4, *P* =0.084). Observation date was significantly and negatively correlated with the proportion of seals bathing (*r* = -0.93, *n* = 4, *P* = 0.034), but not with the proportion away from pools (*r* = 0.83, *n* = 4, *P* = 0.086). Time (hours during day in BST) showed no significant linear correlations with these behaviors, but there was an indication of an increase in the percentage of females bathing during the middle of the day (c. 12-1400 hours BST) for all dates except the 4th (Fig. 3). However, with only four study dates it was not possible to statistically test for any diurnal pattern.

In a stepwise linear regression model with the proportion of females bathing as the dependent variable and a sample size of 4, only date was entered as a significant explanatory variable (Table 2), accounting for 54% of the variation in the proportion of females bathing. The same procedure, but with the proportion of females more than one body length away from a pool as the dependent variable, entered mslp as the only significant explanatory variable, accounting for 70% of the variation in the dependant variable. Thus, more females are found away from pools at lower pressures (wetter conditions). This is confirmed in the correlation of rainfall category and percentage of animals away from pools.

Patterns of seal proximity to pools of water relative to weather conditions

We extracted the distance to their nearest pool of water for all females within the GIS database for all dates during the 1998 breeding season. We used these data (log-transformed) as the dependent variable in a stepwise linear regression model with temperature, dew-point temperature, mslp, wind-speed, date and time as independent variables. Sample size was set to the number of days on which seal distributions were recorded (n = 28). Mslp, temperature and wind-speed were entered as explanatory variables (Table 3). This analysis indicated that females tended to be closer to pools of water at higher pressures (drier conditions), at higher temperatures and at lower wind-speeds (respective Pearson correlation coefficients: -0.15, -0.1, 0.032).

DISCUSSION

This study provides some preliminary behavioral evidence of thermal stress from over-heating in a phocid breeding in the cool and wet temperate conditions of an UK autumn season. Our analyses indicate that females' use of, and proximity to, freshwater pools is correlated with the prevailing weather conditions. In warmer, drier conditions, females tended to aggregate around pools, whilst in colder wetter conditions females tended to disperse away from pools. It must noted however, that our behavioral observations from the video footage were centered on a small group of individuals (making estimation of the proportion of seals in or near pools potentially highly variable) in a relatively small area, on four dates within the breeding season. These limits to the sample severely restrict our ability to discuss the wider implications of these data. However, independent support for these data was provided by our GIS based analysis of the proximity to pools of all breeding females within a large portion of the entire breeding colony and throughout the entire breeding season. This analysis indicates that the patterns of pool usage with respect to prevailing weather conditions are seen at the larger colony scale.

Although these results are limited, they do highlight the need for a more thorough and complete examination of the role of thermoregulation in gray seals breeding in northern temperate conditions.

Evidently , no single weather parameter will precisely predict the usage of pools by seals. Seals may not require access to pools on days with rainfall, colder days or windier days, particularly where the wind blows from a cold direction (North or East at this location). Indeed, wind may play an important role. In Figure 1 the clearest separation of data points is between the calm or mildly breezy days (4^{th}, 7^{th}, 15^{th} of October) and the very windy day (22^{nd} of October). Amongst the three less windy days, separation appears to occur on the basis of temperature, with more seals close to pools on warmer days. Interestingly, fewer females are close to pools on a warm but windy day compared to a considerably colder but far less windy day. This suggests the cooling capacity of strong winds is a significant factor. A similar pattern is shown in Figure 2 with the two dates with intermediate rainfall (4^{th} and 15^{th}) being divided vertically on the basis of temperature. The interplay of the various meteorological parameters could be addressed by linking behavioral studies with direct measures of seal body temperatures (both superficially and internally), ambient temperature and, perhaps more pertinently, measures of radiant load (as bursts of direct sunlight may significantly affect behavior).

In our analysis of the proportion of females bathing, the importance of date possibly reflects the depletion of blubber reserves in females as lactation proceeds, thus reducing thermal stress later in the season. We did not test the effect of stage of lactation directly in this study, as the relatively poor resolution of the video images prevented classification of pup ages and therefore estimation of the stage of lactation. Therefore, in this study we used date as a proxy, however, it would be valuable to conduct a more detailed study of thermoregulatory behavior, in relation to stage of lactation and weather conditions.

The number of females actually in a pool at any one time may be influenced strongly by the relative dominance of individuals, in addition to the prevailing weather conditions. Observations suggested that in some cases specific dominant individuals may monopolize pools for long periods, with less dominant females waiting to gain access around the edge of pools and spending relatively brief periods in pools (PR, NCW pers. obs.). It was not possible to determine relative dominance of the individuals in the video footage due to a lack of interactions. Therefore we used the broader measure of attraction towards pools provided by the observed changes in the proportion of animals more than one body length away from pools.

Phocids are unable to pant (although animals will often open their mouth to aid evaporative heat loss across the respiratory surface) or sweat (Riedman 1990). Therefore thermal radiation provides the most important route for heat dissipation on land (∅ritsland *et al.*1978). Blood is shunted towards thermal windows (poorly insulated areas) and peripheral vessels are dilated to enhance radiative heat loss through superficial cooling. However, if solar radiation heats blood at the skin surface, heat loss by radiation may not be sufficient to prevent the induction of thermal stress on warm days. Bathing in pools of water is likely to be the most efficient method for dissipating excess heat because of the high cooling capacity of water (∅ritsland *et al.*1978, Campagna and Le Boeuf 1988, Riedman 1990). The apparent importance of pools for thermoregulation does not exclude the possibility that water is required for drinking (Kooyman and Drabek 1968; Gentry 1981, Reilly *et al.* 1996, Redman *et al.* in press), indeed, the two processes are inevitably linked. Our own observations (SDT, PPP, PR) confirm that gray seals at North Rona drink from pools.

As shown for several other pinniped species, behavioral responses to thermal stress can have far reaching implications on a breeding colony's social organisation (e.g.: Gentry 1973, Campagna and Le Boeuf 1988, Francis and Boness 1991). During dry periods, when pools are fewer and smaller, the degree of aggregation of individuals will increase compared to during wetter conditions when pools are more abundant or the substrate is generally wetter (Twiss *et al.* 2000, 2001). Such meteorological effects on seal behavior could, therefore, influence interactions between individuals and dynamics within colonies with potential implications for individual reproductive performance (Pomeroy *et al*. 2001).

Here we have examined thermoregulatory behaviours in adult female gray seals only, but it is likely that males too will be subject to overheating on warmer drier days. Males are larger, with generally darker pelage and thicker layers of sub-cutaneous fat. Males have also been observed drinking water from pools (PPP, PR, SDT, SM) at North Rona, and even eating snow on the much colder breeding colony of Sable Island (Canada) in January (SDT). It is possible that potential heat stress has an impact on male gray seal behaviour and territory holding capabilities, as has been demonstrated in some otariid species (Gentry 1973, Campagna and Le Boeuf 1988, Francis and Boness. 1991).

This study provides further evidence of the apparent importance of access to water for gray seals breeding in temperate regions (Twiss *et al.* 2000, 2001, Pomeroy *et al.* 2000, 2001, Redman *et al.* in press), and suggests why water may be so important. It is evident from this and the preceding studies that water is a critical feature of gray seal breeding habitat in the UK.

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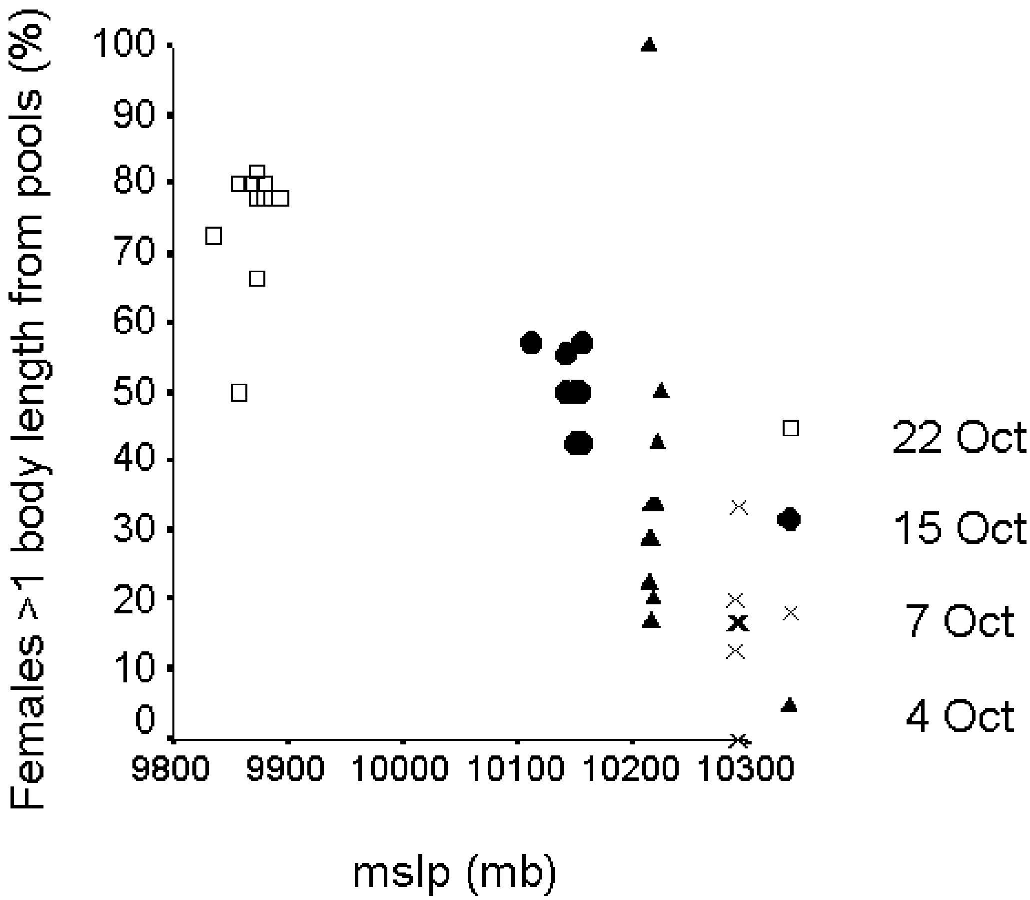
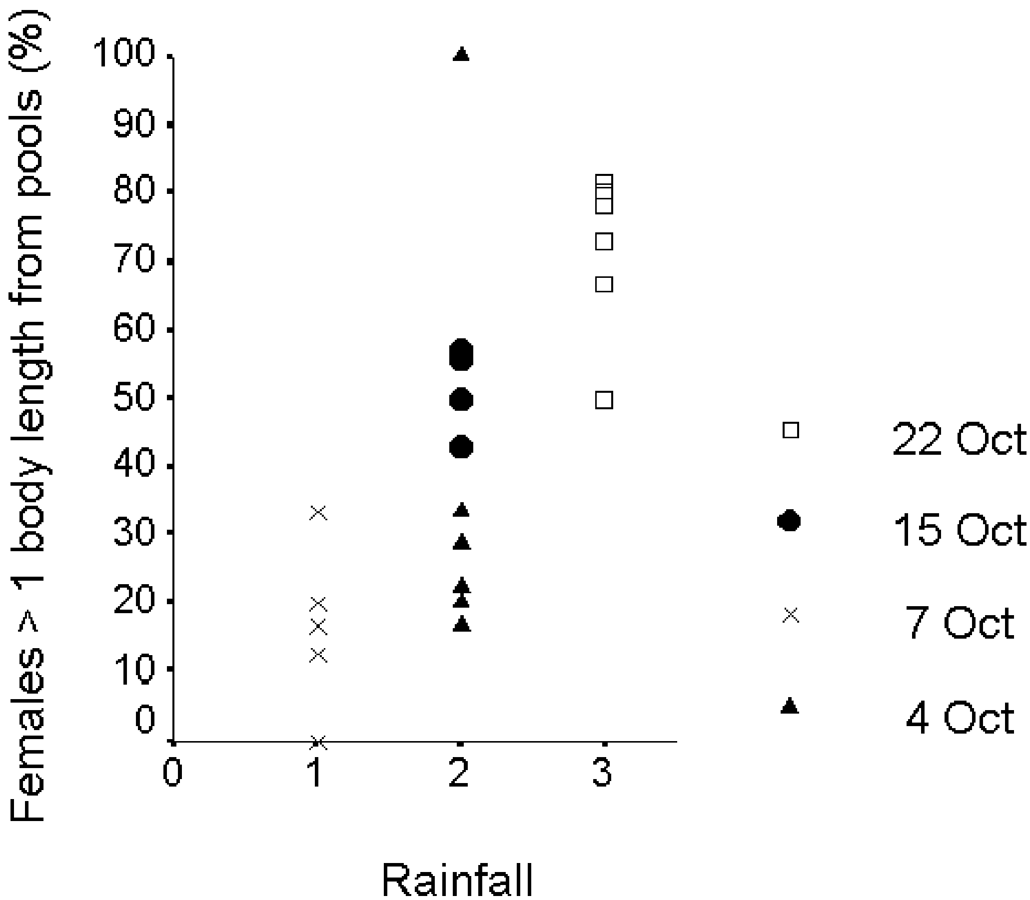
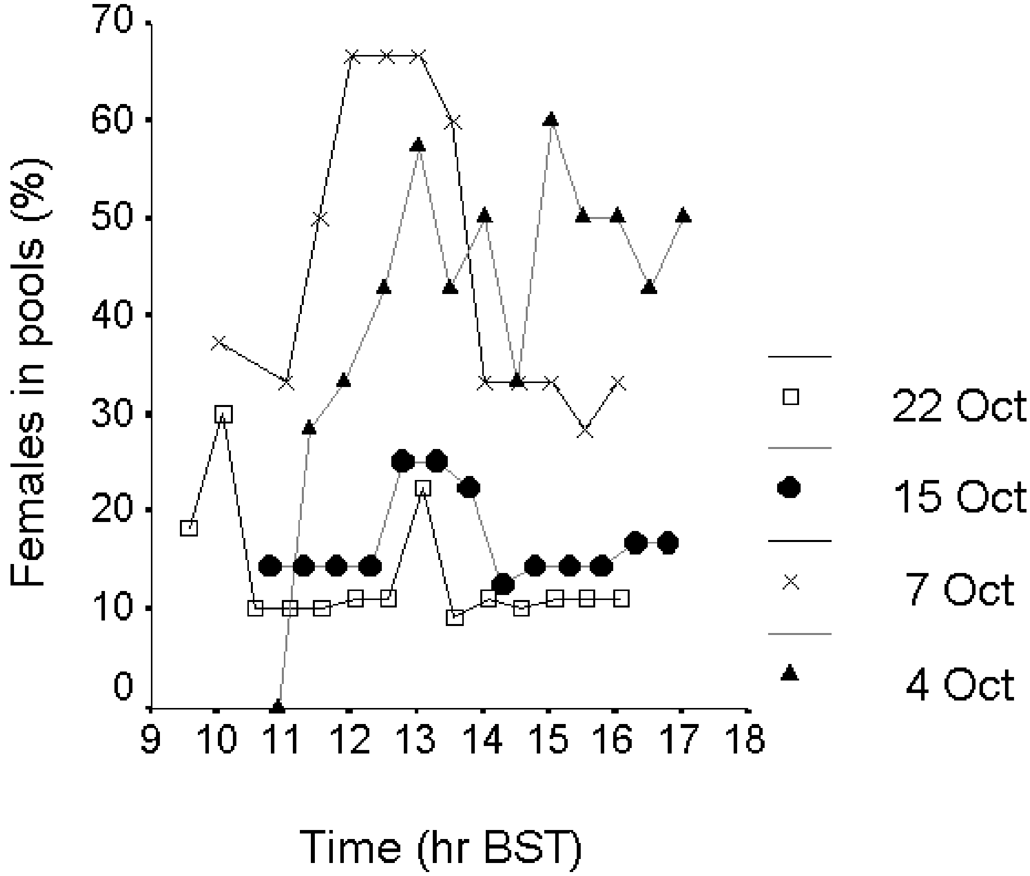
Figure 1. Plot of the percentage of females more than one body length away from a pool of water against mean sea level pressure.

Figure 2. Plot of the percentage of females more than one body length away from a pool of water against rainfall category (1 = dry, 2 = light, 3 = heavy).

Figure 3. Diurnal variation in the percentage of females in pools on each of the four study dates


Females >1 body length from pools (%)
100
90
80
70
60
50
40
30
20
10
0
9800
9900
10000
10100
10200
10300
mslp (mb)
22 Oct
15 Oct
7 Oct
4 Oct


Females > 1 body length from pools (%)
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
Rainfall
22 Oct
15 Oct
7 Oct
4 Oct



Females in pools (%)
70
60
50
40
30
20
10
0
9
10
11
12
13
14
15
16
17
18
Time (hr BST)
22 Oct
15 Oct
7 Oct
4 Oct

Table 1 Mean (±SE) values for meteorological variables on each of the observation dates.

Date in October 1998	4^{th} (n = 13)	7^{th} (n = 12)	15^{th} (n = 9)	22^{nd} (n = 14)
Dry-bulb temperature (^{o}C)	10.32 ± 0.08	10.79 ± 0.09	7.41 ± 2.61	10.30 ± 0.13
Dew-point temp.(^{o}C)	5.65 ± 0.16	7.18 ± 0.18	0.90 ± 0.30	6.51 ± 0.16
Mean sea-level pressure (mb)	10217 ± 0.8	10291 ± 0.6	10146 ± 4.6	9870 ± 3.8
Wind direction (degrees from true north)	76.9 ± 3.5	202.5 ± 4.5	312.2 ± 1.5	230.0 ± 0.0
Wind speed (knots)	16.5 ± 0.4	11.6 ± 0.2	15.0 ± 1.5	41.2 ± 0.8
Rainfall	light	none	light	heavy

Table 2. A summary of linear regression models for the proportion of females bathing and the proportion of females more than one body length from pools. The independent variables were: temperature, dew-point temperature, mslp, wind-speed, date and time (NS = non significant).

	Variables entered	**Adjusted R^2**	**df**	**Sig. *F* Change**
% Bathing	Date	0.54	1,3	< 0.001
	Date & dew-point temperature	0.58	1,2	NS
% Away	mslp	0.70	1,3	< 0.01
	mslp & temperature	0.74	1,2	NS

Table 3. A summary of the linear regression model for the distance to the nearest pool of water for all females within the GIS database for all dates during the 1998 breeding season. The independent variables were: temperature, dew-point temperature, mslp, wind-speed, date and time.

Variables entered	**Adjusted R^2**	**df**	**Sig. F Change**
mslp	0.022	1, 27	< 0.01
mslp & temperature	0.028	1, 26	< 0.01
Mslp & temperature & wind-speed	0.031	1, 25	< 0.01