# A multivariate analysis of phenotype and paternity in male harbor seals, *Phoca vitulina,* at Sable Island, Nova Scotia

**David W. Coltman,**[a] **W. Don Bowen,**[b] **and Jonathan M. Wright**[a]
[a]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3J 4J1, Canada, and [b]Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada

Understanding the links between phenotype and reproductive success is critical to the study of the evolution of mating systems and life-history patterns. We examined the relationship between phenotype and mating success of male harbor seals (*Phoca vitulina concolour*) at Sable Island, Canada. Cluster analyses of eight traits including mating success determined by genetic paternity analysis, haul-out behavior, body mass, and mass change identified four groups of males with distinct characteristics. The most successful males were of moderate body size, were rarely sighted alone, were associated with many different groups on shore, and were sighted on the haul-out relatively infrequently. Large males that hauled out frequently alone, previously thought to be socially dominant, were less likely to be successful. Also less successful were smaller, younger males. Contrary to our hypotheses, and unlike most terrestrially breeding pinnipeds, body size and reproductive effort were not positively associated with mating success, and some successful males appeared to spend considerable time foraging in deep water. *Key words:* body size, mating success, microsatellites, phenotype, pinniped, reproductive strategy, testosterone. *[Behav Ecol 10:169–177 (1999)]*

$I$n polygynous mammals, male reproductive success is largely determined by the number of offspring sired, and thus males compete intensely for mates, whereas females invest more heavily in parental care (Trivers, 1972). Identifying the sources of variation in male mating success is important to our understanding of reproductive strategies and the evolution of sexually dimorphic traits, as phenotypic characteristics that are associated with mating success may be under strong sexual selection. Relatively few empirical studies, however, have identified clear links between phenotype and male mating success in natural populations of large mammals. The studies that have done so usually focus on the importance of social dominance and body size in polygynous systems (e.g., Bercovitch and Nurnberg, 1996; Clutton-Brock et al., 1982; Cowlishaw and Dunbar, 1991; Owen-Smith, 1993).

There are three families of pinnipeds. Of the 18 species in the family Phocidae, 15 species mate aquatically, as does the single species in the Odobenidae. In contrast, all 15 species in the Otariidae generally mate on land (Boness et al., 1993). Among pinnipeds, male reproduction is well understood in the terrestrially breeding species. When mating occurs on land, successful males may maximize mating success by controlling access to females, such as in gray seals, *Halichoerus grypus* (Boness and James, 1979) and northern elephant seals, *Mirounga angustirostris* (Le Boeuf, 1974). Males in other species, such as *Callorhinus ursinus* (Bartholomew and Hoel, 1953), may defend territories within the breeding colony where females aggregate. Male body size is thought to be important in these species for several reasons. In southern elephant seals, *Mirounga leonina,* body size confers a fighting advantage that enables large males to maintain high dominance status (McCann, 1981; Modig, 1996). In other species, large size enables males to prolong their period of tenure through the effect of size on fasting endurance (Lindstedt and Boyce, 1985). Length of tenure has been correlated with mating success in some species (*Arctocephalus gazella*; Arnould and Duck, 1997). In gray and northern elephant seals, body size is also correlated with reproductive effort, which in turn is associated with male mating success (Deutsch et al., 1990; Tinker et al., 1995). Consequently, pronounced size dimorphism is thought to have evolved in terrestrially breeding pinnipeds in response to intense sexual selection on male body size for both competitive and energetic reasons (Bartholomew, 1970).

Phocid seals that mate aquatically are less size dimorphic than Otariid seals and most other polygynous mammals (Weckerly, 1998). It has been suggested that body size is less likely to confer a competitive advantage in the three-dimensional aquatic environment (Bartholomew, 1970). There are scant empirical data on male mating success in aquatically mating phocids to test this idea, however. As phocid seals represent more than half of extant pinniped species, this represents a major gap in our understanding of male reproduction in pinnipeds. On a more general level, the importance of body size to male mating success in these taxa is of basic interest to zoologists, as phocid seals are at the bottom end of a continuum of sexual dimorphism in large mammals (Weckerly, 1998). Aquatically mating pinnipeds compete for mates in a medium in which there is comparatively less potential for males to monopolize females, or resources important to females, which predicts reduced polygyny and potential for sexual selection (Emlen and Oring, 1977).

In this study, we set out to identify the phenotypic traits associated with male mating success in harbor seals (*Phoca vitulina concolour*). The harbor seal is a relatively small-bodied, slightly dimorphic phocid species (males are approximately 7% longer and 20% heavier than postpartum females (Bowen WD, unpublished data; McLaren, 1993) that breeds on isolated islands or beaches along the eastern coast of North

America (Boulva and McLaren, 1979). At Sable Island, females come ashore from the middle of May to early June and wean their pups after an average of 24 days of lactation (Muelbert and Bowen, 1993). Females commence regular foraging trips in mid-lactation (Boness et al., 1994; Thompson et al., 1994) as they become energetically depleted (Bowen et al., 1992). Mating occurs exclusively at sea and is believed to occur in late lactation or shortly following weaning; however, copulations have rarely been witnessed (Thompson, 1988). Males compete intensely for mates: evidence of fighting, lacerations about the head and hindflippers, is seen exclusively during the breeding season (Boulva and McLaren, 1979; Godsell, 1988; Thompson, 1988; Walker and Bowen, 1993). At Sable Island, Coltman et al. (1998b) measured male mating success by paternity analysis using microsatellites and found a low variance in the distribution of paternities. They suggested that the low level of polygyny seen in harbor seals was probably due to the inability of males to monopolize females or predict their movements at sea. Previous research on male reproductive behavior has suggested that social dominance and body size may be important characteristics.

At Miquelon, Perry (1993) found three males that defended aquatic territories through which females had to pass to gain access to the sea sired at least one pup, suggesting that mating may occur near shore with socially dominant males. At Sable Island, Walker and Bowen (1993) identified a group of males that were heavily wounded from fighting with other males, usually hauled out alone, and exhibited fidelity to a single location on the beach. They suggested that these males were socially dominant, an idea also suggested by Boulva and McLaren (1979), and that they may have been reproductively successful by concentrating their aquatic activity in nearby home ranges arrayed in parallel to the beach. By doing so, males were thought to intercept females as they departed and returned from foraging trips in late lactation. Patterns of onshore behavior may therefore provide clues as to which males are socially dominant and/or reproductively successful.

Variation in circulating levels of serum testosterone may also provide information on individual reproductive and dominance status. Elevated levels of testosterone induce seasonal changes in reproductive physiology and behavior (Crews and Moore, 1986; Lincoln, 1989), but circulating levels may also be a consequence of behavior, particularly aggression (Harding, 1981; Wingfield et al., 1990). In some species, it is thought that high serum testosterone levels may be maintained in response to winning social "challenges" or other aggressive behaviors (e.g., Harding, 1981; Wingfield et al., 1990). Other studies have demonstrated positive correlations between serum testosterone levels and social dominance in field studies of mammals (e.g., *Petaurus breviceps*: Stoddart et al., 1994; *Mus musculus*: Zielinski and Vandenbergh, 1993). Bartsh et al. (1992) reported that dominant male Weddell seals maintained higher testosterone levels through the breeding season than defeated or noncompetitive males. We hypothesized that reproductively successful male harbor seals were socially dominant and therefore had higher levels of serum testosterone than other males.

Finally, we sought to investigate the influence of body size on male mating success from an energetic standpoint. Because harbor seals are slightly size dimorphic, body size could influence male mating success. In all animals there is a trade-off between feeding (or the maintenance of body condition) and reproduction when such activities are mutually exclusive (Lindstrom, 1998; Roff, 1992), which may ultimately influence mating success. For example, Berkovitch and Nurnberg (1996) found that paternity in *Macaca mulatta* was modulated by body condition because males with more body fat fed less and invested more effort toward reproduction. We previously hypothesized that body size and the quantity of stored energy may influence male mating success by constraining male reproductive effort rather than by conferring a direct competitive benefit (Coltman et al., 1997, 1998a). Relatively large males, or males in better condition at the beginning of the breeding season, may have an advantage because they can afford to spend more time making shallow dives (Coltman et al., 1997), which are commonly associated with reproductive behavior (Boness et al., unpublished data). Most harbor seals are unable to fast for the duration of the breeding season (Coltman et al., 1998a) and exhibit bouts of diving behavior consistent with offshore feeding trips during the breeding season (Coltman et al., 1997). Thus larger males may feed less, be able to afford to expend more total energy on reproduction, and therefore may have higher encounter rates with potentially receptive females.

In this study, we used multivariate statistical techniques to investigate the relationships between paternity determined genetically (Coltman et al., 1998b) and phenotypic traits of male harbor seals. We hypothesized a mating advantage for large males on energetic grounds and hypothesized that successful males exhibit behavioral and endocrine patterns which have previously been thought to reflect social dominance.

## MATERIALS AND METHODS

### Study site and data collection

The study was conducted during the breeding seasons (mid-May to the end of June) of 1993 and 1994 on the north beach of Sable Island (43°55′ N; 60°00′ W), a partially vegetated sandbar 160 km east of Nova Scotia. A total of 385 and 270 harbor seal females gave birth on both the north and south beaches of Sable Island in 1993 and 1994, respectively. Roughly 70% of the pups were born on the north beach in each year. Males and females show strong fidelity to their breeding beach both within (Godsell, 1988) and between seasons (Bowen WD, unpublished data).

We captured males in nets as described in Bowen et al. (1992) near the beginning of the breeding season (from 20 May to 1 June), at which time we started to collect data on social behavior. In both 1993 and 1994, more than 90% of all births on the north beach occurred between 20 May and 4 June. Seals were individually marked with fluorescent paint on the lower back to facilitate rapid identification during daily beach surveys, and two numbered rototags (Dalton, Henley on Thames) were applied to the hindflippers for permanent identification. We attempted to recapture each male near the end of the breeding season (range 20 June–5 July). At each capture males were weighed with a 200 ± 0.5 kg Salter spring-balance. A dorsal length measurement (i.e., a straight line from tip of the nose to the tip of the tail; McLaren, 1993) was taken on the subset of males used in concurrent studies of diving behavior (Coltman et al., 1997) and energetics (Coltman et al., 1998a). We sedated males (approximately 0.2 mg diazepam per kg body mass) so that a reliable length measurement could be obtained. Body size measurements were also taken from a selection of sedated, known-age males handled during the course of other research to estimate size–age relationships.

We conducted surveys of the north beach daily at approximately 1700 h to locate marked males. Locations of hauled-out males were recorded relative to numbered stakes placed at 0.5-km intervals along the north beach, and social context was noted (either sighted alone or in a group of seals). At Sable Island, most harbor seals are distributed in groups of 1–31 individuals along the 25-km section of north beach study area. For the purpose of this study, we defined a group as a

cluster of animals separated from the next cluster by 100 m or more. Groups are typically separated by distances of 0.5 km or more and tended to form at predictable beach locations within seasons, although the membership of these groups did change (Schaeff et al., 1999). At each capture and during daily beach surveys, we also recorded the presence of fresh wounds on the neck and hindflippers of each male. We stopped collecting observational data during the first week of July.

All males were included in a study of paternity conducted using microsatellites (Coltman et al., 1998a). A likelihood approach was used to assign the paternity of all pups born on the north beach in the following year to candidate males using a simulation program to estimate the degree of statistical confidence in paternity assignment (Marshall et al., 1998). We used data from paternities assigned at 50% and 80% confidence in this study.

### Testosterone assay

We took blood samples for the testosterone assay from a subset of the males. At each capture, 10 ml of whole blood was taken from the extradural vein as quickly as possible, usually within 5 min of capture, to avoid possible antagonistic effects of handling stress on circulating hormone levels. Blood samples were stored without preservative on ice in a cooler until they were processed at the end of the day. Serum was separated by centrifugation of whole blood for 30 min at 3500 rpm and stored at $-20°C$ until assayed.

Assays were performed within 4 months of collection in 1993 and 1994. Total serum testosterone was determined using a commercially available radioimmunoassay system (Testosterone/dihydrotestosterone $^3$H Assay System, Amersham) following the manufacturer's instructions. According to the manufacturer, the only steroid having significant cross-reactivity to the antiserum is dihydrotestosterone (40–50%), hence the measurement of circulating androgen presented here represents total testosterone plus 40–50% of circulating dihydrotestosterone. In most other mammals, levels of circulating dihydrotestosterone are low relative to testosterone (Testosterone/dihydrotestosterone $^3$H Assay System manual, Amersham), but they have never been measured separately in a pinniped. We thus refer to the measured hormone levels simply as testosterone for simplicity.

Steroid hormones were separated by extracting serum diluted 1:4 in distilled water with diethyl ether. The mean extraction recovery of testosterone, estimated from adding serial dilutions of $^3$H-labeled testosterone standard to pooled harbor seal serum, was 92.7% ± 17.9% ($n = 12$). Recoveries indicated that testosterone could be measured accurately in harbor seal serum using this system [testosterone = 1.3($^3$H-labeled added standard) − 0.12; $r^2 = 0.93$, $n = 12$, $p < .001$). The manufacturer reports the sensitivity of the assay to be approximately 3 pg/tube. Intra- and interassay coefficients of variation were estimated to be less than 10% and 17%, ($n = 10$ and 6, respectively). For statistical comparisons, serum testosterone measurements were blocked into four equal time periods according the date they were taken, and differences between groups of seals and over time were tested using repeated-measures ANOVA. If a male had more than one testosterone measurement within a particular time period, the average serum testosterone concentration was used in the ANOVA model, and males lacking an observation in any time period were omitted from the statistical analysis.

### Phenotypic traits and data analysis

The following eight traits describing social behavior, movement, body size and energetics, and mating success were used in a multivariate analysis to classify males into groups of similar phenotypes. These were:

*Social behavior:*
1. Proportion of times sighted alone,
2. Presence or absence of wounds indicating inter-male fighting,
3. Number of different groups in which observed.

*Movement:*
4. Index of haul-out site fidelity (calculated as the standard deviation of haul-out site locations),
5. Proportion of days sighted during daily beach surveys.

*Body size and energetics:*
6. Initial body mass (estimated mass on 20 May, calculated by correcting the first mass measurement by the daily rate of mass change over the interval between 20 May and the date of the actual first mass measurement),
7. Daily rate of mass change (final minus initial body mass, divided by the interval between measurements in days expressed as a percentage of initial body mass).

*Mating success:*
8. Paternity of one or more pups born in the following season at 80% confidence.

We used cluster analysis to identify groups of males with similar phenotype using these eight traits. Before cluster analysis, continuous variables were tested for normality, transformed if necessary, and all data were standardized to a mean of 0 and standard deviation of 1 to ensure measurement on a similar scale and equal weighting. A hierarchical agglomerative cluster analysis of Euclidean distances was performed using Ward's linkage to initially identify data clusters. We then these clusters as the initial data partition for a second cluster analysis by the iterative k-means algorithm to determine final groupings. Inspection of the final data groups then identified traits that were associated with paternity. These traits were used as covariates in a logistic regression model to identify predictors of paternity.

In addition to the eight characteristics used in the cluster analysis, we analyzed additional phenotypic data collected from subsets of study males. These data included diving behavior from time-depth recorders (TDR; $n = 18$; Coltman et al., 1997), energetics from the analysis of stable isotope dilution ($n = 22$; Coltman et al., 1998a), circulating levels of testosterone ($n = 58$ measurements from 12 males in 1993 and 96 measurements from 29 males in 1994), and body length/age ($n = 41$). These data were not used in the cluster analysis due to the reduced sample; thus group differences in age, diving behavior, energetics, and testosterone were analyzed post-hoc. We also included data on paternities assigned at 50% statistical confidence (Coltman et al., 1998b) for post-hoc comparison, however we used the more conservative (80% confidence) data for cluster classification. We compared average individual heterozygosity, calculated as the proportion of heterozygous loci, between groups to ascertain if paternity assignments were biased toward less heterozygous individuals.

All data were checked for normality and transformed if necessary before parametric statistical analyses. The significance of all statistical tests was set at .05. Statistical analyses were performed in MINITAB Release 10 for Windows (Minitab Inc.) or SPSS for Windows version 6.13 (SPSS Inc.).

### RESULTS

Cluster analysis using Ward's linkage identified 4 major groups of individuals among the 68 males studied (39 in 1993 and 29 in 1994; Figure 1). Using these groups as the initial data partition, k-means clustering affirmed these group compositions with the exception of one individual in group C that
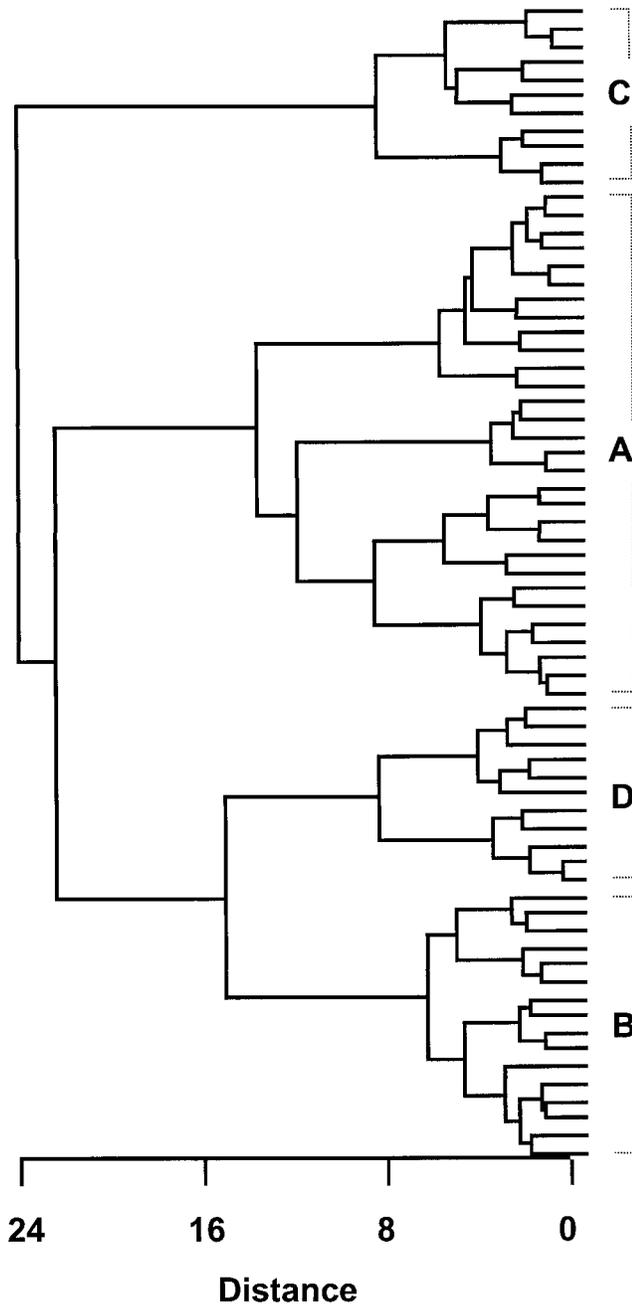
**Figure 1**
Dendogram of observations produced by cluster analysis using Ward's linkage of Euclidean distances. Each observation represents an individual. Four groups (noted A, B, C, and D) with distinct phenotypic characteristics were resolved.

was moved to group D. The defining characteristics of these groups are shown in Table 1.

Group A males most resemble those hypothesized to have been successful in a similar multivariate analysis by Walker and Bowen (1993); they were most frequently sighted alone, showed evidence of fighting, exhibited the highest degree of fidelity to their haul-out location, and associated with few groups. These were also the largest males with the highest mean rate of mass loss. Because mass loss is correlated to initial body mass in breeding male harbor seals (Coltman et al., 1997), we also compared rates of mass loss by ANCOVA to account for the influence of initial body mass. Differences

among groups in rates of mass loss were not statistically significant when differences in initial body mass were accounted for ($F_{3,63} = 2.56$; $p = .06$), thus group B males lost mass at a similar rate relative to their initial body size as other males. Like males of group A, males of group B also exhibited haul-out site fidelity, showed evidence of fighting, and associated with few groups, yet were sighted alone less frequently than group A males and were lighter. Neither group A nor group B included a male with paternity at 80% confidence.

Group C consisted of males that behaved quite differently from A or B males: they tended to be sighted more frequently, showed less fidelity to a single haul-out location, were rarely sighted alone, and associated with more groups. These males were the lightest, and they tended to be shorter. We estimated the age of 37 study males from length measurements (Table 1) by the relation between age and length shown in Figure 2. Tagging information provided the ages of another four study males. The median estimated age of group C (9.0 years, $n = 7$) was less than all other groups combined (median = 12.5 years, $n = 34$; Mann Whitney $U$ test; $U = 54.5$; $p < .05$). Fewer group C males showed evidence of fighting than males in all other groups ($\chi^2 = 4.8$, df = 1; $p = .029$). As with groups A and B, no males in this group were assigned the paternity of a pup born in the following season at 80% confidence.

Group D contained all males that had paternity at 80% confidence. Other characteristics of group D included low frequency of sightings, rarely sighted alone, associated with a moderate number of groups, and absence of strong haul-out site fidelity. Most group D males showed evidence of fighting and were of moderate body size. They were also of similar estimated age (median = 11.5 years; $n = 3$) as males of group A (14.0 years; $n = 22$) and B (12.0 years; $n = 9$). Group D males were assigned significantly more paternities than males of other groups if the confidence level for paternity assignment was relaxed to 50% (Table 1). However, males of group D did not differ significantly in average heterozygosity from other groups (Table 1).

There were significant differences among groups in total body energy content measured at the beginning of the breeding season ($F_{3,19} = 6.70$; $p < .005$). Group A males had significantly more total body energy than males from groups B and C (Figure 3). ANCOVA indicated that group differences in total body energy content could be explained by variation in body mass or general body size rather than variation in body composition (ANCOVA initial mass as covariate, mass effect: $F_{1,18} = 48.7$; $p < .001$, group effect: $F_{3,18} = 1.30$; $p > .05$). Group A males catabolized significantly more total body energy per day (measured as the average daily loss in total body energy) during the breeding season than other males (Figure 4; $F_{3,19} = 6.08$; $p < .005$). Group D males had the highest rate of food energy intake (Figure 4; $F_{3,13} = 4.47$; $p < .05$). Combining energy catabolized from body stores and energy derived from feeding, there was no significant difference between group means in the daily rate of total energy expenditure (Figure 4; $F_{3,13} = 1.73$; $p > .05$). There was also no difference among groups in mass-specific total energy expenditure (group A: $3.70 \pm 0.36$, $n = 6$; group B: $3.68 \pm 0.21$, $n = 4$; group C: $3.29 \pm 0.33$, $n = 5$; group D: $3.60 \pm 0.21$ W/kg, $n = 2$; $F_{3,13} = 0.35$; $p > .05$).

Neither time spent hauled out on shore (Figure 5; following arcsine square-root transformation, $F_{3,15} = 0.58$; $p > .05$), nor time spent in shallow dives (<20 m; following arcsine square-root transformation $F_{3,15} = 2.77$; $p = .08$) derived from the analysis of TDR records (Coltman et al., 1997) differed significantly among groups. However, group A males spent less time making deep dives (>20 m) than other groups (following arcsine square-root transformation, $F_{3,15} = 5.27$; $p < .05$).

Levels of circulating serum testosterone varied greatly with

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**Table 1**

**Characteristics of male harbor seals grouped by cluster analysis**

| | Group A (n = 29) | Group B (n = 17) | Group C (n = 11) | Group D (n = 11) | Test statistic | $p$ |
|---|---|---|---|---|---|---|
| Sighted alone (% of sightings)* | $24.3 \pm 4.7^{xyz}$ | $8.6 \pm 2.4^{x}$ | $1.8 \pm 1.0^{z}$ | $0.8 \pm 0.8^{y}$ | $F_{3,65} = 8.44^{**}$ | <.001 |
| Evidence of fighting* | 22/29 | 16/17 | 5/11 | 9/11 | $\chi^2$ (df = 3) = 6.3 | ns |
| Groups associated with* | $1.7 \pm 0.2^{xy}$ | $1.7 \pm 0.2^{vw}$ | $4.8 \pm 0.4^{wyz}$ | $3.1 \pm 0.5^{vxz}$ | $F_{3,65} = 19.4^{**}$ | <.001 |
| Haul-out site fidelity index (km)* | $1.4 \pm 0.2^{y}$ | $0.8 \pm 0.1^{wx}$ | $3.4 \pm 0.5^{xyz}$ | $2.0 \pm 0.5^{wz}$ | $F_{3,65} = 9.50^{***}$ | <.001 |
| Proportion of days sighted* | $0.38 \pm 0.02^{y}$ | $0.42 \pm 0.03^{x}$ | $0.51 \pm 0.03^{yz}$ | $0.31 \pm 0.04^{z}$ | $F_{3,65} = 5.55$ | <.01 |
| Initial mass (kg)[a] | $116.4 \pm 1.5^{vxy}$ | $101.6 \pm 1.5^{vw}$ | $100.5 \pm 2.5^{yz}$ | $108.6 \pm 2.5^{wxz}$ | $F_{3,65} = 16.6$ | <.001 |
| Rate of mass change (kg/day)* | $-0.62 \pm 0.02^{yz}$ | $-0.42 \pm 0.04^{y}$ | $-0.43 \pm 0.04^{z}$ | $-0.54 \pm 0.04$ | $F_{3,65} = 13.5$ | <.001 |
| Paternities | | | | | | |
|   80% confidence*   0 | 29 | 17 | 11 | 0 | $\chi^2$ (df = 3) = 68.0 | <.01 |
|                1 | 0 | 0 | 0 | 11 | | |
|   50% confidence   0 | 22 | 13 | 8 | 0 | H (df = 3) = 22.0 | <.001 |
|                1 | 7 | 2 | 2 | 7 | | |
|                2 | 0 | 2 | 1 | 2 | | |
|                3 | 0 | 0 | 0 | 2 | | |
| Heterozygosity | $0.60 \pm 0.22$ | $0.61 \pm 0.19$ | $0.67 \pm 0.15$ | $0.67 \pm 0.15$ | $F_{3,65} = 0.65$ | >.05 |
| Mean dorsal length (cm) | $153.9 \pm 1.2$ (n = 22) | $153.9 \pm 1.9$ (n = 9) | $149.6 \pm 1.5$ (n = 7) | $154.3 \pm 0.8$ (n = 3) | $F_{3,37} = 1.64$ | >.05 |

Values are shown $\pm$ 1 SE. Superscripted letters indicate pairs of means that differ significantly (Student-Newman-Keuls multiple comparisons, $p < .05$); ns, not statistically significant.

  * Variables used in multivariate classification.

  ** ANOVA followed arcsine-square root transformation.

*** ANOVA followed logarithmic transformation.

time and among individuals, generally decreasing over the breeding season (Figure 6). Mean levels between 4 and 5 ng/ml were observed early in the breeding season, falling to approximately 1 ng/ml later in the breeding season when estrous females became increasingly available. Patterns were similar among groups (Figure 6), as mean levels decreased significantly with time (repeated measures ANOVA, $F_{3,69} = 34.01$; $p < 0.001$). Variation between groups was not significant overall (repeated measures ANOVA, $F_{3,24} = 1.25$; $p > .05$), nor were the effects of age, initial body mass, nor time of day sampled (data not shown). Compared against groups B, C and D combined, mean levels of serum testosterone among group A males declined to low levels earlier (repeated-measures ANOVA, group-by-time interaction; $F_{9,72} = 4.05$; $p < .01$).

The males of group D stood apart from all other groups in their frequency of sighting and the proportion of times sighted alone, suggesting these characteristics were associated with reproductive success. A logistic regression model incorporating both of these variables as covariates successfully predicted the mating success of 89.7% of all observations [paternity at 80% confidence as response variable: model $\chi^2 = 16.6$, df = 2, $p < .005$; constant = 1.38; $\beta$ (times sighted) = $-6.12$, $p <$
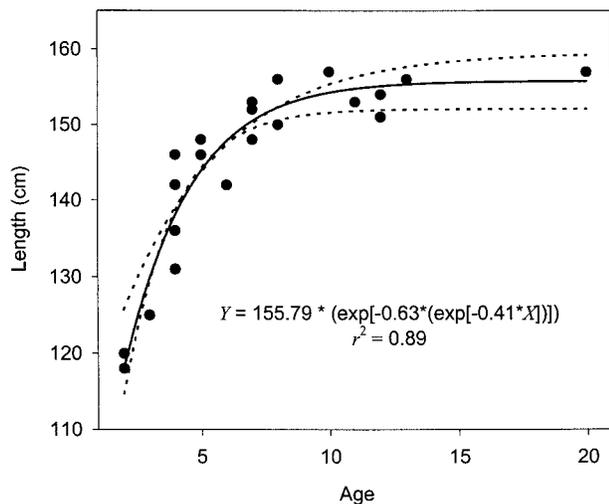


**Figure 2**
Dorsal lengths of live known-age male harbor seals at Sable Island (n = 21). Data were fitted to the Gompertz growth equation used by McLaren (1993) to describe postpubertal growth in pinnipeds: $L_{age} = L_0 * \{exp[a * exp(b * x)]\}$. Dotted lines indicate 95% confidence intervals.

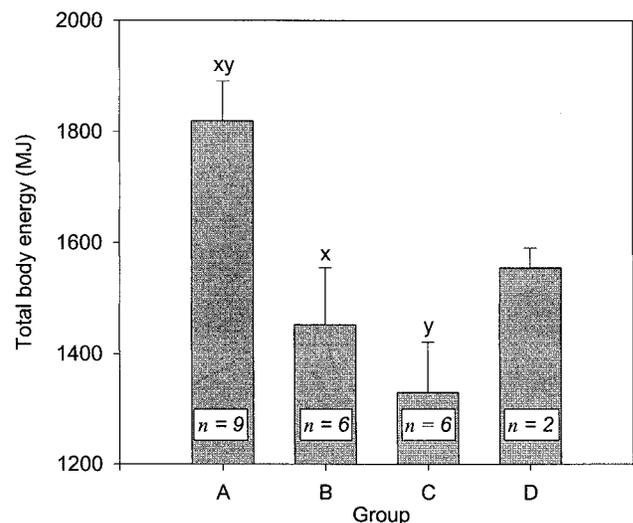$$Y = 155.79 * (exp[-0.63*(exp[-0.41*X])]) $$
$$r^2 = 0.89$$



**Figure 3**
Mean total energy composition of male harbor seals grouped by cluster analysis. Error bars represent 1 SE of the mean, and letters denote means that differ significantly (Student-Newman-Keuls comparisons, $p < .05$). Numbers at the base of columns indicate sample size.
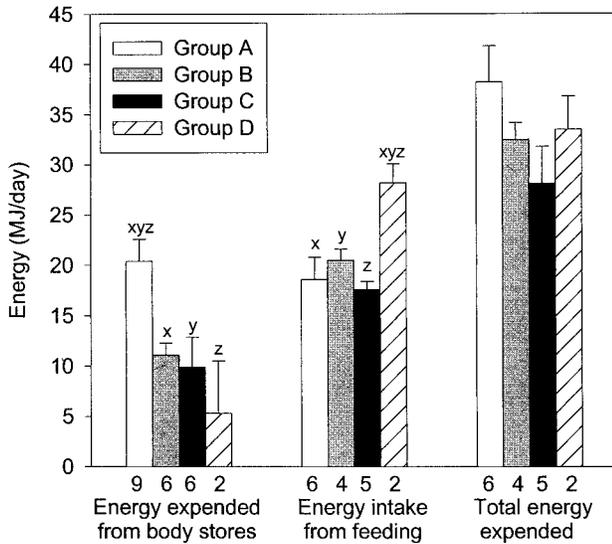
**Figure 4**
Mean sources of energy expenditure of breeding male harbor seals grouped according to phenotype. Error bars represent 1 SE of the mean, and letters denote means that differ significantly (Student-Newman-Keuls comparisons, $p < .05$). Numbers at the base of columns indicate sample size.



**Figure 5**
Diving activity of breeding male harbor seals grouped according to phenotype. Error bars represent 1 SE of the mean, and letters denote means that differ significantly (Student-Newman-Keuls comparisons, $p < .05$). Numbers at the base of columns indicate sample size.

.05; β (times sighted alone, following arcsine transformation) = −6.89, $p < .05$]. The probability of male mating success therefore increases with decreasing frequency of sightings on shore and with decreasing frequency of hauling out alone (Figure 7).

## DISCUSSION

One potential criticism of this study is that the genetic analysis had limited power to detect paternity. Few paternities could be assigned at the 80% confidence level due to the large number of candidate males considered for each pup (paternity was assigned for 4% of all sampled pups at 80% confidence, or for 30.9% of all pups at 50% confidence; Coltman et al. 1998b). Therefore, although most males assigned paternities at 80% confidence were probably successful, we cannot conclude that males of other groups did not sire offspring. Fourteen males from groups A, B, and C would have been assigned paternity of at least one pup if the confidence level in paternity assignment had been relaxed to 50%. However, even at this level of confidence in paternity assignment, males of group D would be assigned the paternity of significantly more offspring than males from other groups (Table 1). Thus it seems reasonable to conclude that group D males were relatively more successful than other males based on the genetic data. We used the 80% confidence paternity data in the multivariate analysis because they are more conservative, given that our study objective was to identify traits associated with success.

One potential source of bias in paternity assignment exists that also could influence these results. Paternity assignment based on maximum likelihood is potentially statistically biased toward individuals that have a large number of homozygous loci (Devlin et al., 1988). However, we found no evidence that this occurred in our data (Coltman et al., 1998b), and there was no significant difference among groups in genetic variation, measured as individual heterozygosity (Table 1).

Group A males most clearly resemble the group of males described by Walker and Bowen (1993) which were hypothe-
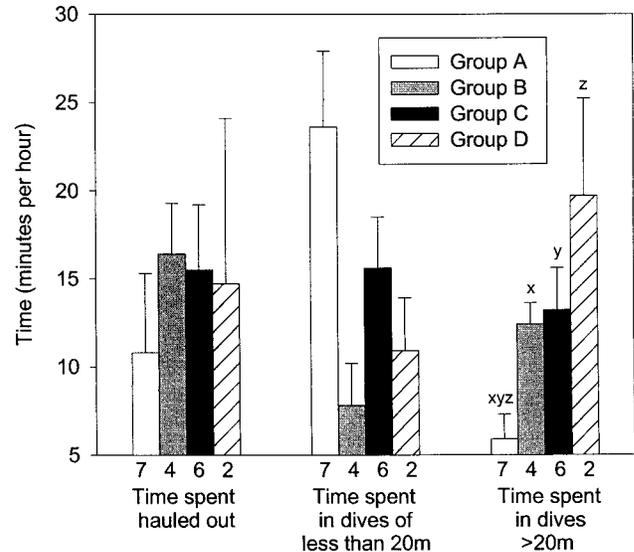
sized to be reproductively successful. These males frequently hauled-out independently of groups at a particular beach site and showed evidence of fighting; however, the genetic data suggest that they were relatively unsuccessful. Group A also contained the largest males. We have previously hypothesized a mating advantage for relatively large males or for those males in good condition at the beginning of the season because large males should be able to fast longer and thus spend more time on reproduction (Coltman et al., 1997, 1998a). Indeed, data from TDRs indicated that group A males spent less time making deep dives (Figure 5), which are more likely to be associated with foraging (Coltman et al., 1997). However, we found no evidence that large body size and the associated differences in aquatic activity (Coltman et al., 1997) were positively associated with mating success. By contrast, data from the only other aquatically mating phocid studied to date indicated that large, territorial Weddell seal males obtained more copulations than smaller males (Bartsh et al., 1992). However, observed copulations may not provide a good measure of paternity. Other studies using genetic estimates of paternity in pinnipeds (gray seals: Amos et al., 1993, 1995; captive harbor seals: Harris et al., 1991) and many other vertebrates (e.g., birds: Birkhead et al., 1990; primates: Berard et al., 1993; ungulates: Pemberton et al., 1992) have found that traits thought to be predictors of mating success were often unreliable.

One possible interpretation of the low mating success in group A males, and perhaps in group B males (Table 1), that consistently hauled-out at the same site is that the wide dispersal of females along the beach at Sable Island resulted in a low probability of encountering females. Evidence for this suggestion comes from the observation (Coltman, 1997) that males were not more likely to mate with females located nearby onshore. An alternative explanation is that males that haul-out alone during the breeding season may do so as a result of defeat in intrasexual competition. Such changes in behavior have been observed in Weddell seals, where males that failed to defend an underwater territory received wounds and spent the majority of the ensuing breeding season hauled out
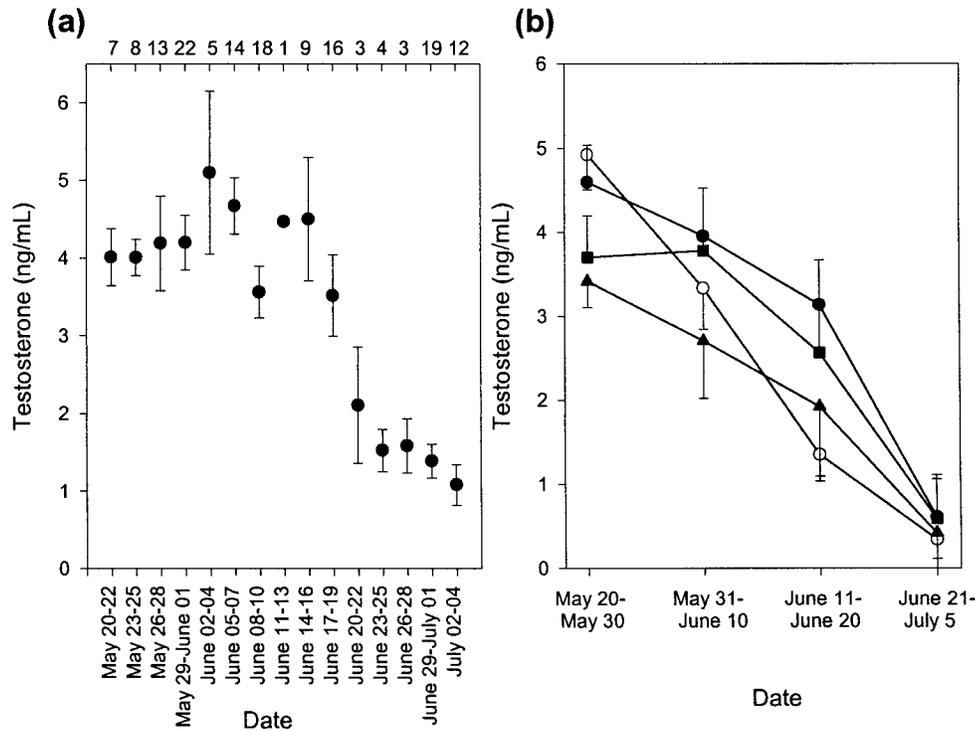
**Figure 6**
(a) Mean (±SE) serum testosterone concentrations of adult male harbor seals during the breeding season. Numbers at the top of indicate the number of males represented in each interval. (b) Testosterone profiles of male harbor seals classified by phenotypic characteristics. Group means (± SE) are indicated by filled circles (group A), open circles (group B), filled triangles (group C), and filled squares (group D). Group sample sizes were $n = 5, 15, 3,$ and $5$, respectively, for the dates listed.

on shore (Bartsh et al., 1992). Bartsh et al. (1992) also found that defeated males showed a marked decline in serum testosterone coincident with their withdrawal from competition, possibly resulting from the stress of defeat. All harbor seals showed a decline in serum testosterone toward the end of the breeding season, a typical pattern among male pinnipeds (Atkinson and Gilmartin, 1992; Bartsh et al., 1992; Noonan et al., 1991). However, group A males showed the most marked decline over the first three time blocks (Figure 6). This resembles the pattern seen in the testosterone profiles of defeated male Weddell seals (Bartsh et al., 1992), suggesting that some males in this group may have been defeated in intrasexual competition. Another possibility is that the rapid decline in these males may result from low encounter rates with estrous females (Harding, 1981).

Group C and D males hauled out with more groups and at

more sites than males of group A and B. Group C may contain younger males than other groups, as they were lighter, shorter, and had a lower incidence of lacerations resulting from fighting than other males. Both mass and length continue to increase after male harbor seals become reproductively mature (McLaren, 1993; Figure 2); and males thought to be subadult have previously been shown to differ in their behavior during the breeding season, in the way group C differs from other groups (Walker and Bowen, 1993). Walker and Bowen (1993) found that subadult males rarely show evidence of wounding and show less site fidelity than adult males. Both of these observations are consistent with the differences between group C and other males (Table 1). Nevertheless, group C males are likely to be reproductively mature, as they showed similar levels of circulating testosterone as other males (Figure 6). Lack of breeding experience may explain the relatively low success of group C.

Why were group D males more successful? Survey data suggest that they spent more time at sea where the chances of encountering females must be enhanced. In this regard, they behaved like the most successful Weddell seal males (Bartsh et al., 1992). Our data from TDRs do not support this suggestion, as group D males spent similar time hauled out on shore as other males (Figure 5); however, this conclusion lacks power due to the small sample size of successful males with diving records ($n = 2$). Furthermore, time of day may be more relevant than total time at sea given the diurnal diving patterns of females (Boness et al., 1994). Group D males showed little site fidelity and associated with more female groups on shore compared to groups A and B, suggesting that the more successful males may encounter more females while out at sea, on average, than other adult males. This may enable group D males to monitor the breeding condition of a greater number of females on shore than males that either remain with the same group or haul-out at the same site each day.

The mass change and energetic data did not suggest a positive association between body size and/or reproductive effort
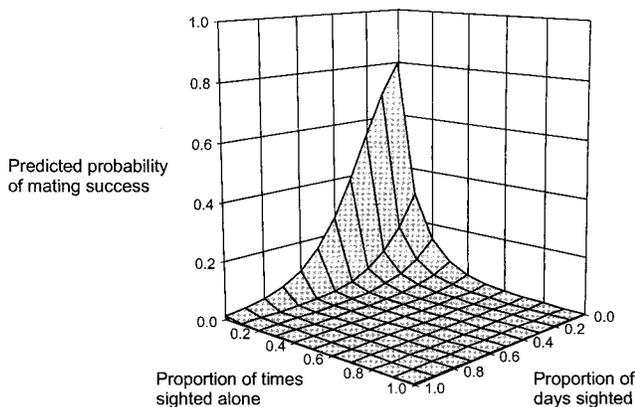


**Figure 7**
Probability of mating success of male harbor seals at Sable Island as a function of number of times sighted on shore during daily beach surveys and the proportion of times sighted alone predicted by logistic regression analysis.

with mating success, as has been found in some terrestrially breeding pinnipeds (Anderson and Fedak, 1985; Deutsch et al., 1990; Tinker et al., 1995). The lack of a body size effect is somewhat surprising given the importance of body size in the other aquatically mating species that has been studied to date, namely, the Weddell seal (Bartsh et al., 1992). We suggest that body size is of lesser importance to mating success in harbor seals than it is in Weddell seals primarily because neither females nor resources important to females can be defended by harbor seal males. In contrast, the most successful Weddell seal males defend underwater territories and breathing holes that females require for access to the sea.

The energetic data indicated that two group D males had a relatively high rate of food energy intake (Figure 4) and dove deeply more often than other males (Figure 5), suggesting that they spent more time on offshore foraging trips. At a site with a low density of females at the haul-out, it may be more profitable to visit the foraging grounds used by females rather than trying to intercept them near the shore. Telemetry data from harbor seals in the Moray Firth, Scotland, suggests that some males adopt the strategy of staying near offshore foraging grounds,, while others focus their activity near haul-out sites during the breeding season (Van Parijs et al., 1996).

Mating systems theory predicts that where groups of females are indefensible and group memberships and/or locations are unpredictable, males may either rove in search of females or patrol territories smaller than female home ranges (Clutton-Brock, 1989). This situation predicts low variance in male reproductive success (Emlen and Oring, 1977). The variation in diving behavior and movement by males among sites where females haul out on the beach suggests that successful male harbor seals use several tactics to obtain matings in this population. The tactic used by a male may depend on body condition at the beginning of the breeding season: males that have large energy reserves can afford to make fewer foraging trips and remain in a home range near shore, concentrating their activity in shallow diving behavior near the haul-out site. Other males may spend more time at sea near foraging locations. The payoff of these tactics may vary depending on the number of breeding females present at the colony within a season and their distribution while at sea. When female density is low near the haul-out site, it may prove less profitable to display (e.g., vocalize) in nearshore waters than to do so at offshore areas where females feed. During our study, the density of breeding females was approximately twofold lower than it had been in previous years (Bowen WD, unpublished data). Perhaps in previous years of higher female density nearshore, males in better body condition that spent much of their time displaying in shallow water had a disproportionately better mating success. Over the two seasons in our study, males that were successful in one year where not necessarily successful the next (Coltman et al., 1998b). However, at this point we do not know if this was because the most successful tactic varies over time or whether males used different tactics in different years. Longer term paternity and behavioral data would be required to test these ideas.

In our study, the behavioral characteristics significantly associated with mating success were being rarely sighted and rarely hauling out alone (Figure 7), making the successful males perhaps the least conspicuous. It could be argued that these same characteristics make these males the most difficult to sample, in which case our sample might be biased toward less successful males. However, we did not find evidence for a large number of paternal half-sibs within cohorts (Coltman et al., 1998b), indicating that it is unlikely that a small number of unsampled males were highly successful. Also, the number of paternities actually assigned was not considerably different

from the expected number, estimated by simulation under the assumption that all sampled males were equally likely to be the true father (Coltman et al., 1998b). Therefore, although there is the potential for bias in our sample, we found no evidence that the effects were considerable.

In summary, the most successful male harbor seals were of moderate body size, associated with many groups of females on shore, and showed limited fidelity to a particular haul-out site. Some successful males spent considerable time foraging in deeper water and thus may have encountered mates at offshore foraging grounds in addition to those encountered while competing for mates closer to the breeding colony. We have determined some of the phenotypic traits associated with paternity in this aquatically mating species. However, unmeasured factors such as previous breeding experience, the intensity or frequency of underwater vocalizations (Hanggi and Schusterman, 1994) and other courtship behaviors, and the at-sea distribution patterns of males in relation to receptive females also may be important predictors of male mating success.

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