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Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights

Michael P. Haley*

Biology Board of Studies, University of California at Santa Cruz, Santa Cruz, CA 95064, USA

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Abstract. The effect of resource-holding power (RHP) and prior residency asymmetries on fight outcome and subsequent seasonal copulatory success was analyzed for fights between marked male northern elephant seals (*Mirounga angustirostris*). RHP asymmetries were measured as differences in estimated mass and prior residency asymmetries were measured as differences in beach tenure prior to the fight. The principal results were: (a) Neither differences in mass nor differences in beach tenure had any effect on fight outcome as separate factors. (b) Mass and tenure differences had an interactive effect on fight outcome; fight winners were either heavier males present for shorter periods (intruders) or lighter males present for longer periods (prior residents). (c) Winners of fights copulated more often than losers after a fight throughout the breeding season; this difference was smallest for low-ranking males, larger for high-ranking males in short fights, and greatest for high-ranking males in long fights. (d) Prior resident males who won long fights obtained significantly more copulations after a fight than the males they defeated, but this was not true for intruder males who won long fights. These results suggest that male northern elephant seals will incur greater contest costs (i.e., fight for longer periods and/or against heavier males) for higher reproductive payoffs. They also imply that, at least for males in long fights, differences in prior residence represent payoff asymmetries, with higher reproductive payoffs for winning prior residents than for winning intruders.

Key words: Elephant seals – *Mirounga angustirostris* – Fighting behaviour

Introduction

Evolutionarily stable strategy (ESS) models divide animal contests into two different types. In symmetrical contests, both contestants are evenly matched, and the contest should be a war of attrition, with the outcome dependent upon which individual is prepared to fight longer (Maynard Smith 1974). In asymmetrical contests, the outcome of a contest should be dependent on the nature and strength of the asymmetry (Maynard Smith and Parker 1976). Two fundamental types of asymmetries that have been proposed are resource-holding power (RHP) asymmetries (Parker 1974), or differences in fighting ability, and payoff asymmetries, or differences in the consequences of winning or losing the contest for the two contestants (Maynard Smith and Parker 1976).

Most contests in nature should be asymmetrical (Maynard Smith and Parker 1976), and further models and empirical studies have refined predictions for asymmetrical contests. If different asymmetries predict opposite outcomes, Hammerstein (1981) argued that decisions about escalation or retreat should be based upon one "dominant" asymmetry. If asymmetries are difficult to perceive, the length of contests may be increased in order to gain reliable information (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983); for example Austad (1983) showed that spider contests were short when the contestants were very different in size, but were much longer when contestants were closely matched in size. If contest costs are low, animals may engage in bouts of fighting while attempting to gain information about asymmetries, and this may lead to an asymmetrical war of attrition (Hammerstein and Parker 1982; see also Marden and Waage 1990), or each bout may be an escalation of the previous bout, until reliable information has been obtained (the sequential assessment model; Enquist and Leimar 1983, 1987; Leimar and Enquist 1984).

In many species the prior owner of a resource is more likely to win contests over that resource (e.g., Riechert 1979; Davies 1978; Sigursjøndottir and Parker 1981; Holberton et al. 1990). This prior resident advantage (Maynard Smith and Parker 1976) has been interpreted in several ways. First, there may be no differences be-

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* *Present address:* Department of Zoology, University of the West Indies, Mona, Kg.7, Jamaica, W.I.

tween prior owners and intruders, but ownership is used as a convention (an uncorrelated asymmetry) for contest settlement (Maynard Smith 1974). Second, prior owners are either stronger or are better fighters than intruders (Leimar and Enquist 1984), and therefore prior ownership corresponds to an RHP asymmetry. Third, the resource may be more valuable to the owner than the intruder (Leimar and Enquist 1984), and therefore prior ownership corresponds to a payoff asymmetry. Fourth, owners may know more about the value of the resource and be prepared to fight hard for it, while intruders may have little or no information about the resource and are not prepared to fight as hard (Enquist and Leimar 1987).

In one context, however, Grafen (1987) has argued that asymmetries are irrelevant to contest strategy. He suggested that if the outcome of a fight was of critical importance, an animal's strategy should not depend on any RHP asymmetries (the "desperado effect"). Simply, if an animal's opportunity to mate is determined by very few fights, then it should fight hard even if its opponent is much bigger.

I studied fights between male northern elephant seals (*Mirounga angustirostris*) in order to see whether the patterns revealed fit any of these theoretical predictions. More specifically, the aims of this study were (i) to measure how RHP asymmetries (measured as differences in mass) and prior residence influence fight outcome between male northern elephant seals, (ii) to see whether fight winners obtained more copulations after a fight than fight losers, and (iii) to determine the influence of dominance rank on fighting strategies, since male dominance rank is positively correlated with copulatory success (Le Boeuf 1974; Haley 1990; Haley et al. in press).

Methods

Background information on northern elephant seals

The northern elephant seal is a highly sexually dimorphic polygynous pinniped; males develop rugose, scarred chest shields and elongated noses, and adult males are 2–8 times heavier than adult females (Deutsch 1990). They breed during the winter (December–March) at rookeries along or off the western coasts of the United States and Baja California. Male elephant seals appear at the breeding rookeries first, during December, and about 20% remain until March, when all the females have departed (Le Boeuf and Reiter 1988). Females arrive in late December and January (peak female numbers occur in late January), give birth to a single pup 6–7 days after arrival, nurse for an average of 28 days, and then leave the rookery (Le Boeuf et al. 1972). Females typically copulate with males during the last 3–5 days of lactation, with the peak copulatory period occurring in mid-February (Le Boeuf 1972). Both males and females fast the entire time they are on the rookery, living off stored blubber, and losing approximately 36% of their arrival body mass over the season (Deutsch et al. 1990). Males who arrive at the rookery late therefore usually weigh more than males of the same age who arrived earlier.

The male population during the breeding season consists of males 5–14 years old, and includes sexually mature but physically immature subadults (5–7 years old). Males (primarily adults and the older subadults) establish a seasonal dominance hierachy by fighting amongst themselves, and dominance rank is positively correlated with copulatory success (Le Boeuf 1974; Haley 1990; Haley et al. in press). Fights are usually only observed once between the same two males in a single breeding season, and dominance rank is consequently fairly stable over the season, although some reversals occur (Haley 1990). Dominance is maintained by agonistic behaviour that includes chases, threat postures and individually distinct vocalizations (Le Boeuf 1974; Shipley et al. 1981). Fights and displays occur throughout the breeding season, although they peak in late January and become relatively infrequent towards the end of the season.

Male tenure on the breeding beaches varies considerably. Although all male size and age classes can be found on the beaches during December, most of the youngest and many of the older subadults are quickly driven off the breeding beaches by older males. Males continue to arrive throughout January and February (Le Boeuf 1974). During the breeding season, some males move around from beach to beach within the rookery, while others remain at a single breeding beach for all or most of the season (Le Boeuf 1974).

Males fight for access to females rather than territory. Although an alpha male can maintain exclusive access to a small harem (<50 females; Le Boeuf 1974; Le Boeuf and Reiter 1988), males do not usually defend specific locations, but typically move around within the harems, or on the harem periphery, engaging in agonistic encounters and attempting to copulate with females. Fights and other agonistic interactions may occur anywhere on the rookery, whether females are nearby or not.

Study methods

This study was conducted on Beach 17, Año Nuevo Island, San Mateo, California, during three winter breeding seasons (1984–1986). Beach 17 is the largest breeding aggregation of elephant seals at the Año Nuevo rookery, and contained approximately 150 males and 800 females at peak season in late January during the study period. All males in this study were individually identified by names marked on the pelage using a mixture of Wellite cream bleach and 30% hydrogen peroxide (Le Boeuf and Peterson 1969). From a blind overlooking Beach 17, behavioural observations of agonistic and copulatory behaviour were taken almost continuously during daylight hours, from late December to early March of each year.

Fights between marked males were videotaped. The length of the fight was determined by measuring the time elapsed from the first blow struck to the point at which one male retracted his nose in a submissive posture and retreated. For each male involved in a fight, the following information was obtained: estimated mass of each male on the day of the fight, beach tenure prior to the fight, copulatory success subsequent to the fight, and dominance rank of each male, as explained below. Dominance rank information was gathered for males in 89 fights, complete data was gathered for 73 fights, and an additional 8 fights in which information on either dominance rank ($n=4$) or mass ($n=4$) was unavailable were also analyzed; sample sizes are therefore different in different sections of the analysis. The males in this sample were approximately 7–13 years old (i.e., mostly adults with a few older subadults).

Mass estimation. Mass was estimated using a photogrammetrical technique (Haley et al. 1991). Photographs were taken of sleeping males stretched out over packed sand, with a marked surveying pole held over the midline of the animal for reference. The area of the male in the photograph was determined using a digitizer (GTCO Digi-Pad 5, GTCO Corp, Rockville, Md., USA), and mass was estimated from the correlation between area (x) and mass (y) ($y=507.74\,x^{1.54}$, $r^2=0.92$; Haley et al. 1991).

Mass estimation photographs were taken throughout the season, whenever the opportunity arose, and thus a photograph could be before, after or on the day of a fight. To calculate mass on the day of a fight, rates of mass loss for each male were estimated using the relationship between length^3 (a function of lean body mass) and mass loss per day (MLD) ($y=-86.87+91.42\,x-31.85\,x^2+3.84\,x^3$, $r^2=0.68$, where x=length and y=MLD; Deutsch et al. 1990). Length was also determined from the photographs, measuring from the indentation at the base of the nose to the base of the hindflipper (c. 90% standard length). Using MLD, and the number of days between fight and photograph (n), the mass estimate for a particular male on the date he was photographed was converted to an estimate for that male on the date(s) he was videotaped fighting, by adding or subtracting MLD$\times n$ to or from the original mass estimate.

Prior residence. All researchers working on both Año Nuevo Island and nearby mainland sites attempted to mark males as soon they arrived; newly arrived elephant seals had a characteristic yellow diatomaceous growth around the eyes. Once a day, the name and position of each male at Año Nuevo was noted on a location chart. Tenure on beach 17 was determined as the number of days the male had been observed present on the beach prior to a fight. For each fight, the male with greater tenure was defined as the prior resident, while his opponent was defined as the intruder.

Copulatory success. Copulatory success was measured as the estimated number of females inseminated (ENFI) (Le Boeuf 1972). ENFI was calculated as the number of successful copulations observed for a male in a harem, divided by the total number of copulations observed in the harem, and multiplied by the total number of females in the harem. Copulations were regarded as successful only if penile intromission lasted 1.5 min (Le Boeuf 1972).

For this study, the number of copulations observed after each fight (over the remainder of the breeding season) for each males was converted into subsequent ENFI. Each fight in this data set was between an unique pair of males and was therefore treated as an unique event (fights are rarely observed between the same males in the same breeding season; Haley et al. in press), and therefore if a male was observed fighting several times his subsequent seasonal ENFI was calculated after each of these fights.

Calculation of dominance index. Dominance rank was determined from the outcome of fights and other agonistic interactions between males. All interactions where one male retreated from another were noted. A dominance index for each male was calculated using the Bradley-Terry (BT) model from the method of paired comparisons (Boyd and Silk 1983), based upon 2570 and 4848 dominance interactions (recorded over the entire rookery) in 1985 and 1986, respectively. (BT indices were not determined in 1984, as observations were *ad libitum*.) This method utilizes a recursive algorithm to generate a value for each male based on these interactions, and comparison of values between two males represents the likelihood that one male will dominate the other (Boyd and Silk 1983). BT indices approach zero for high-ranking males and are large (10–20, depending on the year) for low-ranking males.

The BT index has several advantages over the more conventional ranking based on a dominant-subordinate matrix. The most important of these advantages for this study was that many pairs of low-ranking males on Beach 17 were never observed interacting (although all males had some agonistic interactions); the BT method calculated indices for these males whereas assigning relative rank order using the conventional technique was difficult and subjective. The BT index was in close agreement with the conventional matrix ranking for high-ranking males (e.g., 1985: $r_s=0.791$, $n=20$, $P<0.001$). For clarity, where discussion of the BT index was pertinent, the numerical values are converted to percentile rank.

Results

Fight description and length

Fights consisted of males pushing and shoving against each other chest to chest, while each attempted to strike his opponent on the head, chest or front flippers. Successful blows consisted of open-mouth strikes landing directly on an opponent. Some males followed successful blows by grasping and tugging at the opponent's skin. Unsuccessful blows consisted of strikes that either missed the opponent completely, or were deflected by the opponent's neck and chest. Fights were terminated when one opponent retracted his distended nose and retreated.

Most fights observed were very short. Two-thirds (66.3%) lasted less than 30 s, and almost half of these fights (30.4% of total) lasted less than 10 s. Fights less than a minute in length were characterized by a continuous exchange of blows by both contestants. In longer fights, blow exchange was interspersed with periods where males leaned against each other without moving, or lay on the ground. This behaviour first appeared 1–2 min into the fight. In order to provide a non-arbitrary distinction in the subsequent analysis, short fights are characterized as fights with a continuous exchange of blows, while long fights consist of bouts of blow exchange interspersed with periods of leaning or lying on the ground.

Does dominance rank influence fight length?

Although all ranks of males engaged in short fights, only high-ranking males fought in long fights (Fig. 1). The longest fights were fought by the highest-ranking males (Fig. 1). In 1985 males in long fights had BT indi-

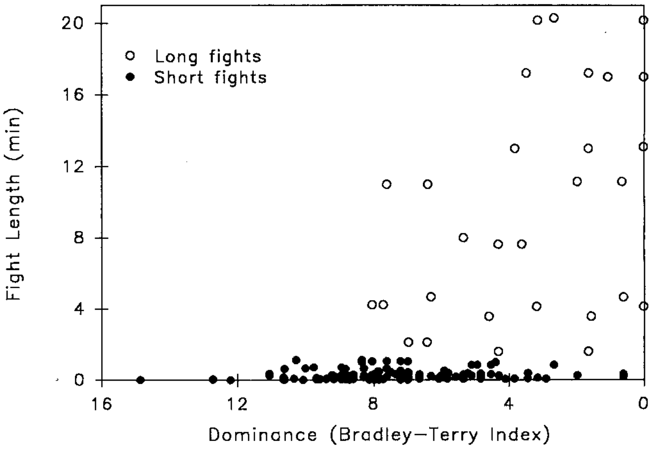

Fig. 1. Fight length and dominance (Bradley-Terry index), for 89 fights (1985–1986). Fights from different years are combined for illustration only. Fights in 1984 are not included as BT indices were not determined in that year. The division between low rank and high rank (see text) was at rank 7.2 (1985) and 8.5 (1986). Note that for most (but not all) of the fights there are two dominance ranks and one fight length per fight. (*Open circles* long fights, *solid circles* short fights)

ces between 0 and 7.2 (i.e., males in the upper 45% of the dominance hierachy), and in 1986 between 0 and 8.5 (upper 42.5%). Since high-ranking males have a larger repertoire of fighting strategies (and also because they can obtain more copulations than low-ranking males; Haley et al. in press), fights were divided into three categories: long fights between high ranking males (i.e., BT index between 0 and 7.2 in 1985, and 0 and 8.5 in 1986), short fights between high-ranking males, and short fights between low-ranking males (i.e., BT indices greater than 7.2 and 8.5 in 1985 and 1986, respectively, corresponding to males in the lower 55% and 57.5% of the dominance hierachy). If a short fight had one high-ranking and one low-ranking male, it was classified as a short fight between high-ranking males. Since there was no systematic attempt to observe agonistic interactions in 1983, BT indices were not calculated for males in that year, and only four long fights in 1983 involving alpha males are included in this study. These fights were categorized as long fights between high-ranking males.

Do mass and tenure differences influence fight outcome?

Heavier males were not more or less likely to win fights with opponents, over a large range of differences in mass. The null hypothesis that there was no difference in mass between winners and losers was not rejected, for all categories of fights (two-tailed paired sample t-test, $n=18$, 17 and 42 for long and short high-ranking and short low-ranking fights, respectively, $P>0.05$ for each category). Differences in mass between winners and losers ranged from -500 to $+600$ kg.

Males who had been present on Beach 17 for longer prior to a fight (prior residents) than their opponents (intruders) were also not more or less likely to win fights. The null hypothesis that there was no difference in tenure between winners and losers was not rejected (two-tailed paired sample t-test, $n=20$, 18, and 43, $P>0.05$ in each case). Differences in tenure between winners and losers ranged from -65 to $+64$ days.

Mass difference and tenure differences had an interactive effect upon fight outcome. The association between mass differences and tenure differences was non-random (Fisher's exact test, $P<0.001$) such that fight winners were usually either heavier intruding males, or lighter prior residents (Fig. 2). In fact there was a negative linear correlation between mass differences (x) and tenure differences (y), particularly for high ranking males (Fig. 3). The correlation for short fights between low ranking males was weaker ($y=0.068-0.032\,x$, $n=43$, $r=-0.347$, $P<0.01$). In general, therefore, the larger the mass differences were between opponents, the larger the tenure differences were (in the opposite direction), or vice versa. Simply, if a male defeated a much heavier opponent, he had been present for a much longer period (or vice versa), whereas if he defeated a slightly heavier opponent, the difference in tenure was usually not as large.

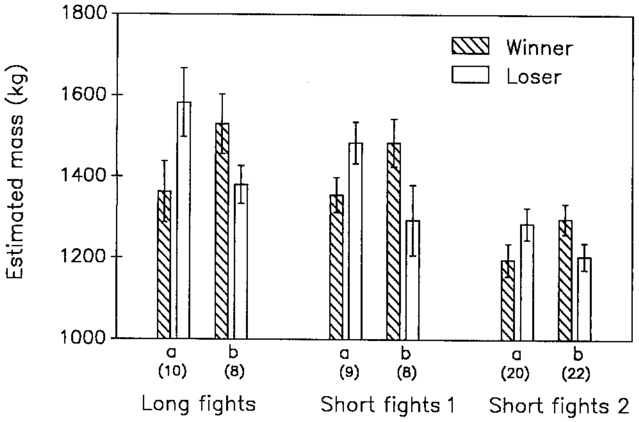

Fig. 2. Mean estimated mass (±SE) of winning (*hatched columns*) and losing (*open columns*) elephant seal males in different fight categories, for 77 fights (1984–1986). *Long fights* fights in which resting behaviour was observed (all males were high ranking). *Short fights 1* fights between high-ranking males where no resting behaviour was observed. *Short fights 2* fights between low-ranking males where no resting behaviour was observed. *a* prior resident male won fight. *b* prior resident male lost fight. *Sample sizes* in parentheses. All mean differences between winners and losers were significant (two-tailed paired sample t-test, $P<0.05$)

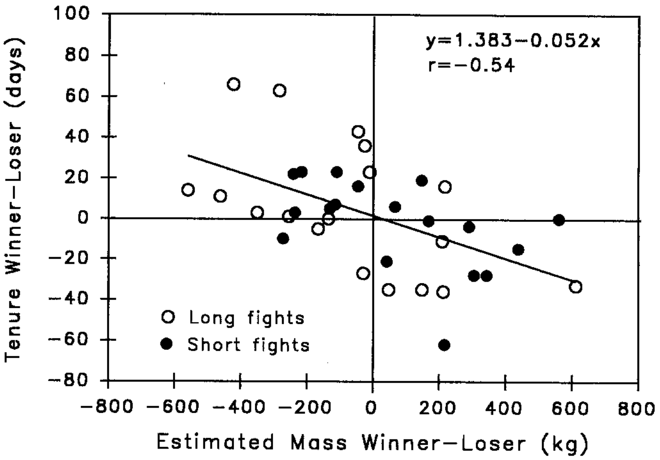

Fig. 3. Relationship between estimated mass difference (winner − loser) and difference in the number of days each male was present on the beach prior to a fight for 37 fights (1984–1986) between high ranking males. $y=1.383–0.052\,x$, $r=-0.54$. (*Open circles* long fights, *solid circles* short fights)

Do males gain reproductive advantages by winning fights?

The hypothesis that the males gained reproductive benefits by winning fights was tested by comparing the estimated number of females inseminated after each fight for winners and losers in each fight category. Within each category, winners of long fights and high-ranking winners of short fights obtained more copulations than losers over the remainder of the breeding season (one-tailed paired sample t-test, $n=20$ and 18, $P<0.05$ in each case) (Fig. 4a). When the probabilities for all categories were combined, winners obtained more subsequent copulations than losers after each fight (consensus

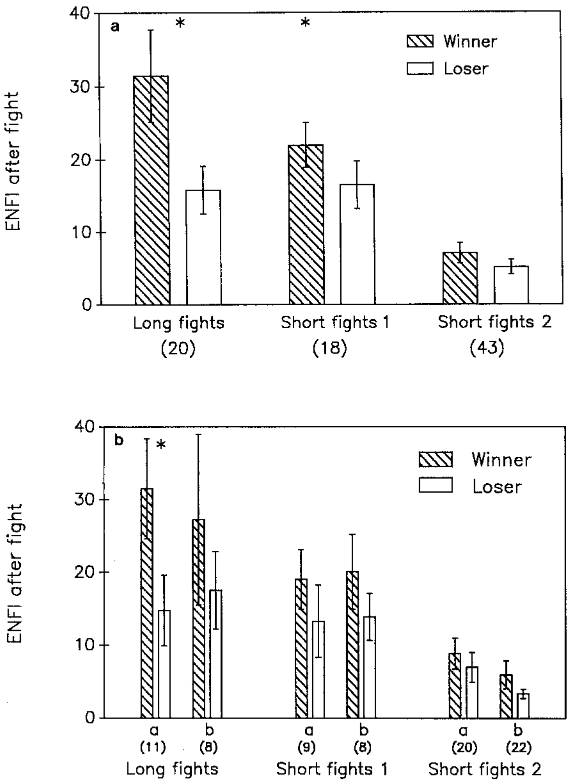

Fig. 4a. Mean estimated number of females inseminated (±SE) after each fight for males in different fight categories, for 81 fights (1984–1986) (*hatched columns* winners, *open columns* losers). **b** As before with fights additionally categorized into cases where the prior resident won or lost, for 78 fights between 1984 and 1986. Sample sizes in Fig. 4a and b are not the same because 3 fights in which the males had equal tenure are excluded from 4b. *Long fights* are fights in which resting behaviour was observed (all males were high-ranking). *Short fights 1* fights between high-ranking males where no resting behaviour was observed. *Short fights 2* fights between low-ranking males where no resting behaviour was observed. *a* prior resident male won fight, *b* prior resident male lost fight. *Sample sizes* in parentheses. * significant difference between winners and losers (one-tailed paired sample *t*-test, $P<0.05$)

combined *P*-value test [Rice 1990], $P<0.005$) (Fig. 4b). These data support the hypothesis that males gain reproductive benefits by winning fights, and demonstrate that high-ranking males who win long fights benefit the most.

When these data were further partitioned into differences between prior resident winners and intruding losers, and vice versa, winners again copulated more often than losers for all fights (consensus combined *P*-value test, $P<0.02$). The only individually significant result, however, was for the difference between prior resident winners and intruding losers in long fights (one-tailed paired sample *t*-test, $P<0.05$) (Fig. 4b). For intruding winners and prior resident losers in long fights, the difference was not significant, because of the large variability in subsequent ENFI for intruding winners (Fig. 4b). These data suggest that prior resident males who win long fights benefit the most.

Discussion

The main results of this study were as follows. First, and most surprising, fight winners were not, on average, heavier than losers; mass is still important in fights, however, in that winning intruders were usually heavier than their opponents, while prior resident winners were usually lighter than their opponents. Second, fight winners gained more subsequent copulations than fight losers, and this difference was greatest for high-ranking males in long fights. Third, for long fights, prior resident winners achieved significantly more subsequent copulations than their opponents, but winning intruders did not. These results can be integrated both with existing information on northern elephant seals and theoretical contest models.

Length of fight and reproductive payoff

Long fights in male northern elephant seals are energetically costly; males who engaged in such fights appeared tired towards the end of the fight, respiratory rates were elevated after long fights (Deutsch 1990), and males often rested for long periods after the fight. In addition, when engaged in a long fight, males ignored copulatory attempts by other males with the females they had previously been defending, and often when recovering afterwards (C. Deutsch unpublished data; personal observation). The results here suggest that these energetic and reproductive costs will only be incurred if balances by a high reproductive payoff; subsequent ENFI values were highest for winning males in long fights (Fig. 4a).

This interpretation is further supported by differences in payoffs for long and short fights for high-ranking males. Dominance rank is positively correlated with copulatory frequency in male northern elephant seals (Le Boeuf 1974; Haley 1990; Haley et al. in press), and only males in the upper 42–45% of the dominance hierarchy fought in long fights. Some fights between high-ranking males were short, and the difference in mean subsequent ENFI for these fights was less than the difference for long fights, suggesting that the decision to engage in a long fight for a high-ranking male may be a function of the relative improvement in reproductive success as a consequence of winning the fight. For example, defeating a male of equivalent rank probably will not improve an individual's reproductive success as much as fighting and defeating the alpha male. Long fights should therefore be more likely in the latter case. Length of contest can similarly be a function of resource value in some species (e.g., Clutton-Brock et al. 1979; Verrell 1986), although not in others (e.g., Englund and Olsson 1990).

RHP asymmetries and prior residence

The fact that there was no overall difference in the mean weight of winners and losers was unexpected, as larger, heavier individuals usually win fights in many other species (e.g., Austad 1983; Wells 1988; Englund and Olsson

1990; Enquist et al. 1990; Dugatkin and Ohlsen 1990), and it was surprising that heavier adult male elephant seals did not have a clear advantage over lighter males in fights that were partly pushing and shoving matches. Another possible RHP asymmetry, the difference in the number or pattern of blows exchanged, is also not related to fight outcome (Haley 1990). One possible interpretation is that mass differences do not represent RHP asymmetries and are irrelevant to fight outcome in elephant seals, and that the relationship between mass differences and tenure differences (Fig. 3) merely reflects the fact that males do not eat while on the beach and so lose weight continuously as they metabolize fat reserves (Deutsch et al. 1990). However, this hypothesis makes it difficult to explain why dominance rank is positively correlated with mass in male northern elephant seals (Haley 1990; Haley et al. in press).

An explanation more consistent with the data presented here is that both being larger and being a prior resident constitute an advantage in a fight, and that RHP asymmetries (i.e., mass differences) are opposed by prior residency advantages in the majority of fights. Fights between heavier prior residents and lighter intruders (i.e., where the asymmetries did not oppose each other) were infrequent (Fig. 3), suggesting that agonistic encounters between such individuals do not usually culminate in fights. Fights were usually won by either heavier intruders or lighter prior residents, and the negative correlations between mass differences and tenure differences indicate that larger differences in mass were necessary to compensate for larger differences in tenure (or vice versa), particularly for high ranking males. These correlations suggest the outcome of male elephant seal fights is dependent upon one asymmetry outweighing the other, consistent with the prediction of Hammerstein (1981) that fight outcomes should be dependent upon a single dominant asymmetry. Hammerstein's models defined the conditions under which one asymmetry or another will be dominant; such conditions, if they exist, are not obvious for male elephant seal fights.

One potential objection to the interpretation that mass differences and tenure differences have an interactive effect upon fight outcome is that this might be an artefact of the methodology used to estimate mass. Specifically, one could argue that as the error of the estimate increases with the number of days between the initial photograph and the fight, it could be that the correlation between mass and tenure differences is an artefact of the increased error for mass estimates for long-term residents (if, for example, long-term residents lose mass more slowly than intruders). There are three reasons to suspect this argument is not justified. First, fights where skinny longer-term residents defeated observably larger intruders were often noted and discussed by field workers. Second, high-ranking individuals lose mass faster than low-ranking individuals (Deutsch et al. 1990), and so it is unlikely that the mass estimation technique falsely inflates the rate of mass loss for high-ranking long-term residents. Lastly, the period between the photographs and the fights was independent of the tenure status of the males (Methods), and so there is no reason to attribute greater error in mass estimates for long-term residents than for intruders.

Prior residence and payoff asymmetries

Prior residency may correspond to a payoff asymmetry, as suggested by Leimar and Enquist (1984), for at least some males in this species. In long fights, winning prior resident males obtained more subsequent copulations than their opponents, while high variability in subsequent payoffs for winning intruding males made higher payoffs for these males less predictable (Fig. 4b). Even though the small sample sizes for these categories make it difficult to draw firm conclusions, the above interpretation is consistent with other aspects of male elephant seal behaviour; winning prior residents maintain their dominance position, but as dominance is established by dyadic interactions between males (Le Boeuf 1974; Haley 1990), the intruder who wins does not automatically take over a prior resident's dominance rank and access to females.

A difference in payoffs was less evident for short fights, although the mean subsequent ENFI of winners was still greater than losers. This smaller difference may be the reason that high-ranking males do not continue fighting for long periods, as suggested above. In addition, the reproductive opportunities of low ranking males are more constrained than high-ranking males (Le Boeuf 1974; Haley 1990; Haley et al. in press), and consequently the ability of low-ranking males to improve their reproductive opportunities by defeating other low ranking males is limited. Mass differences were still negatively correlated with tenure differences for the winners of short fights, however, although the effect was less marked for low-ranking males. This implies that a male's decision to terminate or continue a short fight is partly based upon these two factors, even though the likelihood of improving his reproductive success is lower than for long fights.

Attempting to find immediate reproductive payoffs for short fights may be inappropriate. Only seasonal copulatory success was measured here, because the marked names were lost each year in the seasonal summer moult, but other studies of tagged males have demonstrated that the few successful individuals improve their dominance status and subsequent copulatory success over successive years (Clinton 1990; Clinton and Le Boeuf 1993; see Le Boeuf and Reiter 1988). Short fights (particularly for low-ranking males) probably represent attempts to gain experience and possibly "ratchet" up the dominance hierachy, over successive years. In this context it is logical that prior residence is still an advantage in short fights because subsequent dominance status is less predictable for intruding winners, as for males in long fights.

Consistency of results with theoretical models

Unlike long fights in some species (e.g., Englund and Olsson 1990; Enquist et al. 1990), long fights in male elephant seals did not fit predictions of the sequential assessment model (Enquist and Leimer 1983, 1987, 1990; Leimar and Enquist 1984). Specifically, long fights with large RHP asymmetries do not end in an earlier phase than fights with smaller asymmetries, and individuals do not proceed through a series of escalations while attempting to gain information about each other. If anything, the intensity of blow exchange during different "bouts" in long fights degrades over the course of the fight as the animals become tired. There was no evidence that fight contestants were assessing their opponents' fighting ability during the course of a fight by judging their ability or frequency in landing blows, as there was no detectable difference in the pattern of blow exchange between winners and losers (Haley 1990). Nor are long fights an example of the "desperado effect" (Grafen 1987); this implies that the variance in RHP asymmetries would increase as the reproductive payoff increases, but the variance in mass asymmetries was the same in all fight categories (*F*-test, $P > 0.05$ for all comparisons).

Long fights in male elephant seals resemble an asymmetrical war of attrition (Hammerstein and Parker 1982). This is suggested by three lines of evidence. First, the pattern of blow exchange did not affect the outcome of the fight (Haley 1990), but individuals who won long fights were the males who persisted longer. It was not uncommon, for example, to see a male in a long fight, who had been consistently driven backwards and frequently struck with vigorous blows, suddenly win when his opponent gave up and retreated. Second, the interactive effect between mass and prior residence asymmetries implies that male northern elephant seals' decisions about how long to fight are influenced both by differences in mass and by how long they have been present on the breeding beaches. Third, the greater variance in subsequent reproductive success for intruding winners in long fights, compared to prior resident winners, suggests that the advantages to longer residency are that prior residents have more to gain by winning in long fights than intruders, as argued above.

Hammerstein and Parker (1982) argued that contestants in an asymmetric war of attrition will base decisions on how long to continue a contest on the ratio of contest benefits to contest costs. This is consistent with the above interpretation that fights are influenced by mass and residency asymmetries; the energetic costs of fighting a larger male are probably greater than fighting a smaller male, and a prior resident in a long fight gains more reproductive advantages by winning than an intruder. It is not clear, however, exactly how these decisions are made. While a male can probably easily assess differences in mass once a fight begins, it seems unlikely that he can consistently assess differences in residence; sometimes this may be obvious as a newly arrived intruder will have a previously unheard trumpet call, while at other times long fights occur between individuals that have been interacting for several weeks, and it seems unconvincing to suggest that an individual remembers when each of the other males arrived on the beach (particularly on a large breeding beach like Beach 17). I suggest that a male's decision about how long to fight is made on the basis of (a) mass asymmetries, and (b) his potential reproductive payoff, as indicated by his residency period and dominance rank (and possibly by the number of copulations before the fight, although this is unlikely, since many fights occur well before the peak copulatory period; Le Boeuf 1972; Deutsch 1990).

A male's assessment of how long an opponent is prepared to fight may only be made by fighting until he himself is prepared to stop, so he probably cannot judge any payoff asymmetries at the beginning of a fight. Even if payoff asymmetry information is not immediately available to the contestants, however, if differences in expected payoffs mean different decisions about how long to continue, as suggested here, the outcome of a fight will be a result of both RHP and payoff asymmetries.

At least two additional factors, not addressed in this study, may affect the theoretical interpretation of these results. First, although some conclusions can be tentatively drawn from these results about the nature of the assessment that occurs at the beginning of a fight, the assessment that occurs before a fight may also be important, during the trumpeting displays. Although these displays seem to function as a mechanism for individual recognition (see Shipley et al. 1981) other forms of assessment, such as visual assessment of size, may also occur, and this may affect fighting strategy. Second, and perhaps more important, age may also influence fighting strategy. Age could only be approximated for males in this study, but other studies of elephant seals (Clinton 1990; Clinton and Le Boeuf 1993; Le Boeuf and Reiter 1988) have shown that the peak in male copulatory success occurs around 10–13 years old. Although mean reproductive effort (as measured by percentage mass loss) is constant for all males after age 6 (Deutsch et al., in press), this reproductive peak still may affect an individual's fighting strategy; a high-ranking 13-year-old male, for example, might be prepared to fight for longer than a younger male with the same mass and residency, since he would be unlikely to have as many reproductive opportunities in succeeding years. If true, long fights for older males could be an example of the "desperado effect" (Grafen 1987). Additionally, since male elephant seals may live up to 14 years old (Clinton and Le Boeuf 1993; Le Boeuf and Reiter 1988), it is likely that individual experience varies considerably, and that differences in individual experience influence individual fighting strategies. This may further help to explain the variation in fighting behaviour observed in this species.

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