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An Analysis of Aggression and Sexual Displays in the Humboldt Penguin (*Spheniscus humboldti*)

ABSTRACT: Humboldt penguins (*Spheniscus humboldti*) are a colonial species of *Spheniscidae* that inhabit the coastal regions of Peru and Chile, and in those regions their breeding ranges overlap both spatially and temporally with one other penguin species, the Magellanic penguin (*Spheniscus magellanicus*). Humboldt penguins are monomorphic and monogamous breeders. Twelve captive Humboldt penguins (6 males, 5 females and 1 unsexed penguin) were studied in an enclosure during the winter of 1995 (1 February - 20 April, 62 total hours). A study of these penguins included the examination of 1) behaviours that provoked aggression, 2) aggressive interactions between individuals, 3) the maintenance of pair bonds, 4) the relative frequency of sexual displays in successfully mated and unsuccessfully mated pairs and 5) the social integration of the unsexed juvenile penguin.

Data collected regarding the aggression between individuals demonstrate that aggression ended after two exchanges. Thus, aggression was proposed to involve a binary system of interaction, including the initiation and the termination of those acts. Results from this study offer general support for cost-benefit analysis theory that aggression is an expensive means of resolving dispute. Through the study, there were 129 aggressive turns, 105 initial acts of aggression with 24 aggressive responses. In 81 cases, a "retreat" or "no response" was recorded as the termination of an aggressive bout.

Observations of pair maintenance include the following: 1) data regarding pair formation and successful mating in the Humboldts does not support the Richdale (1951) observations that successful mating is marked by a decrease in the number of sexual displays and 2) the hypothesis that frequency of ecstatic display indicates the physical attractiveness of males was not fully supported. Observations reveal that successfully mated males displayed more numerous in certain cases where unsuccessfully paired males displayed less numerous. Additionally, the rate of display in males did not predict breeding status or physical attractiveness to the female. Certain males displayed more frequently than did successfully paired and mated males, while others displayed at the same rate as successfully mated males and remained unpaired.

An 11 month old juvenile of undetermined sex was closely observed during this study. Data collected over the three month period record the aggressive behaviour, sexual behaviour, play and feeding behaviour in this individual. The data reveal that this juvenile was the most deferent individual and was the recipient of more aggression than any other individual. Behavioural evidence for sex determination was inconclusive in this study.

Key Words: aggressive turns, binary aggression, pair maintenance, social integration

INTRODUCTION: The genus *Spheniscus* contains four members: the Magellanic penguin (*Spheniscus magellanicus*), the Galapagos penguin (*Spheniscus mendiculus*), the African penguin (*Spheniscus demersus*) and the Humboldt penguin (*Spheniscus humboldti*). These four species maintain extensive morphological similarities despite the continental distance that separates the African penguin from the other three South American species. The Humboldt penguin encounters only one other member of *Spheniscus*, the Magellanic penguin. Interspecific pairing and mating does not occur when the two species overlap spatially and temporally during

their breeding windows (Johnson, 1972), and it has been suggested that they cannot be conspecific (Johnson, 1972) despite the fact that *S. humboldti* - *S. demersus* (Conway, 1965) and *S. demersus* - *S. magellanicus* (Junker, 1945) hybrids have been observed and bred successfully.

During all seasons, Humboldt penguins are inshore feeders, foraging on small fish and crustaceans, primarily euphausiids and other cephalopods. Like many other Sphenisciformes, Humboldt penguins circle around their prey and attack by the side, swallowing it head first before moving on to the next (Stonehouse, 1975; Hales & Welch, 1994).

When on land, Humboldt penguins commonly live in burrows that are composed of soil, rocks and more extensively, guano; to complete the nest, Humboldts gather twigs, stones, grass and other human deposits for nesting material (Murphy, 1936). Like many other colonial avian species, breeding in the Humboldts is somewhat synchronized; however, breeding is not entirely limited to specific times of the year. Nonetheless, there are two visible breeding peaks, and these peaks coincide with the availability of food and of nesting sites (Campbell, 1985). Egg laying occurs throughout the year.

Like many penguins (Jouventin, 1972), Humboldt pairs contact each other through extensive visual and vocal signals. The maintenance of the pair bond is essential since the availability of food is highly positively correlated with the coastal weather patterns and oceanic tides; two individuals are required to successfully rear offspring. These conditions may predispose the Humboldt to its relatively high degree of monogamy. It is this monogamous relationship that requires recognition. This demand is intense enough to cause same sex pairs to appear throughout the colonies.

Despite the relative accessibility of this penguin species, Humboldts remain one of the least studied spheniscids and unfortunately, this places the fate of the species into question. Human activity, including commercial fishing and guano collection, in addition to egg poaching, has drastically reduced the Humboldt penguin population. In 1981, the U.S. Department of the Interior declared the Humboldt penguin endangered and suggested a population density of 14,500-18,000 birds (Hayes, unpublished data 1981) in the wild and a density of 136 captive birds in the United States (McCusker, 1985). Because the Humboldts are consistently threatened in

this manner, it is essential that programs be initiated to aide this species in recovering its lost numbers.

In this study, I attempt to interpret several Humboldt penguin behaviours, including aggression between individuals and sexes, the maintenance of pair bonds and the integration of the juvenile into the group. I hope to establish a table of exchanges with respect to aggression so that responses to aggressive acts may be categorized into a binary system. I also hope to establish the dominant individuals in this group by examining the level of aggression and its frequency. Additionally, I set out to examine the displays between sexes, specifically to test the Richdale observations that the rate of sexual display is decreased in successfully mated pairs. Finally, I wish to observe the integration of the juvenile into the group and to determine the sex of this penguin vis-à-vis behavioural cues. This study was conducted at the Philadelphia Zoo.

METHODS

Subjects: This study was performed on 12 captive Humboldt penguins (Table 1), monitored in conjunction with the Director of Ornithology of the Philadelphia Zoo. This group of penguins comprises individuals on loan from Sea World, San Diego and the Milwaukee Zoo. For identification purposes, all penguins were tagged above a flipper. Each male was tagged on the right flipper while each female was tagged on the left flipper. Birds were sexed by DNA analysis from blood samples. These bands were removed periodically to relieve the stresses of post nuptial and seasonal molts. In this group, birds ranged from 3 to 6 years (subadults) and 6 to 17 years (adults). Of the 12 penguins, 6 were subadults (4 males, 2 females), 5 were adults (2 males, 3 females) and the final penguin was an 11 month old juvenile whose sex was at the beginning of observation undetermined.

Table 1: Subjects at the Philadelphia Zoo

Subjects	Relative Age	Status
Blue Right	Subadult	Paired
White Left	Adult	Paired
Orange Right	Subadult	Unpaired
Juvenile	Juvenile	Unpaired
Yellow Right	Adult	Mated
Blue Left	Adult	Mated
Green Right	Adult	Paired
Pink Right	Subadult	Paired
Yellow Left	Subadult	Paired
Red Left	Subadult	Paired
Black Left	Adult	Mated
Purple Right	Subadult	Mated

Subjects were provided with an enclosure that was atypical of the barren Peruvian climate; tussock grass replaced the native bushes and trees and nesting coves were located above ground, and relatively few stones were provided for nesting foundations. The enclosure was partitioned by a stream which emptied into a larger communal pool. The penguins were fed around 0900 hours and 1500 hours daily. Diet consisted of various small fish, typically eviscerated and supplemented with vitamins.

Procedure: From 1 February through 20 April 1995 (62 hours of observation), the Humboldt Penguins were observed, and data were recorded regarding the aggressive interactions and the actions which elicited aggression in all penguins. Additionally, data were recorded regarding the maintenance of pair social relationships. A study on a smaller scale included observing the social integration of the juvenile penguin.

Observations were taken from the south side of the enclosure. Penguins residing in the nesting coves were not visible; however, at all other times, penguins were in full view and could be distinguished on the basis of their flipper bands.

Data tables consisted of three sections: sexual displays given by individuals, aggressive acts followed by the response of the targeted individual, and finally, the actions which provoked these aggressive turns. No effort was made to determine the frequency of such aggressive interactions.

Definitions:

- *Bill-to-Axilla*: Focal penguin places head under either flipper and raises opposite flipper. Focal penguin will lower opposite flipper during display and may growl. This is a form of aggression.
- *Sideways Stare*: Focal penguin peers with one eye at another individual. This is a form of aggression.
- *Alternate Stare*: Focal penguin alternates view from side-to-side. This is a form of aggression.
- *Pointing*: Focal penguin leans forward to threaten a nearby individual. Beak may be open or closed.
- *Gape*: Focal penguin points to threaten object and emits a harsh braying sound.
- *Beaking*: Penguins lock bills and engage in tugging bouts while grunting.
- *Ecstatic display*: Focal penguin rotates bill skyward, takes several deep breaths and emits a braying call while arching flippers backward. This is a sexual display.
- *Mutual display*: Penguins face one another and emit harsh calls mixed with grunts. This a form of greeting and pair maintenance.
- *Mutual trumpet*: Penguins stand side-by-side and bray simultaneously while leaning forward. This act is performed by pairs.
- *Vertical Head Movement*: Focal penguin jerks head up and through the motion of an “infinity” symbol. This act seems to be a sexual display and indicate territory.

Statistical Analysis: Chi-square tests for statistical significance with 11 degrees of freedom.

See Appendix for table.

RESULTS:

Aggression: Although data could not be recorded for every act of aggression, 46 of the 129 acts of aggression were traced to the causes of aggressive bouts. In these cases, it was observed that five behaviours elicited aggression: **proximity** (focal penguin acts aggressively toward another penguin that violates its “personal space”), **en passant** (focal penguin acts aggressively toward another penguin while the locomoting penguin passes within personal space), **foraging** (competition for food elicits aggression in nearby penguins), **nesting area violations** (focal penguin acts aggressively toward another invading the nesting “territory”) and **mate disturbance** (focal penguin acts aggressively toward individual displaying near focal bird's mate).

Data tabulated (Table 2) for observations reveal that penguins employed the most aggressive acts (charges and attacks) when invading penguins attempted to transgress into the nesting territory and when invading penguins displayed to or near already paired individuals. The data also demonstrate that penguins violating the “personal space” or penguins passing too close to other individuals received the least aggressive turns in response to this behaviour. Medium scale aggression was reserved for times of foraging when competition for food was presumably high.

Table 2: Causes of Aggression

Causes ->	Proximity	En Passent	Foraging	Nesting Area	Mate Disturbance	
Aggression						
Bill to Axilla	0	0	0	0	0	
Sideways Stare	2	0	0	0	0	
Alternate Stare	1	0	0	0	0	
Point	0	3	0	0	0	
Gape	0	2	0	0	0	
Peck	0	0	18	0	0	
Beaking	7	0	0	0	0	
Charge	0	0	0	4	4	
Attack	0	0	0	3	2	
TOTALS	10	5	18	7	6	46

On a larger scale, a study involved observing aggression and the direct responses to those acts. Observations made over the three month period involve 129 complete acts of aggression. These acts involve 105 *directed* acts of aggression and 24 aggressive responses to

those directed acts. Of the 105 initial acts of aggression, 51 (48.6%) of those acts were followed by retreats, stand downs or turning away (all labeled as a “retreat”) and 30 of the 105 acts (28.6%) elicited no responses (maintained grounds, continued doing same activity - anything but retreat or return aggression). Because acts of aggression elicited non-aggressive responses (81 of 105 acts for 77.1%) and the remaining 24 acts of aggression terminated any exchange between individuals, a binary system of aggression in Humboldt penguins could be established (Table 3).

Table 3: Binary System of Aggression

	Response												Total
First Act	B-t-A	Side	Alt	Pnt	Gap	Peck	Beak	Chg	Att	Retreat	None		
Bill to Axilla	0	0	0	0	0	0	0	0	0	0	4		4
Sideways	0	3	0	0	0	0	0	0	0	2	3		8
Alternate	0	1	0	0	0	0	0	0	0	1	6		8
Point	0	0	0	6	0	0	0	0	0	8	9		23
Gape	0	0	0	0	2	0	0	0	0	4	1		7
Peck	0	0	0	0	0	7	0	0	0	21	7		35
Beaking	0	0	0	0	0	0	5	0	0	2	0		7
Charge	0	0	0	0	0	0	0	0	0	9	0		9
Attack	0	0	0	0	0	0	0	0	0	4	0		4
Total Init.	0	4	0	6	2	7	5	0	0	51	30		105
Total Resp													24
Total Turns													129

The tabulation of this data on an individual basis demonstrates the levels of aggression in this group of penguins (Table 4). Both *blue-right* and *yellow-right* initiated statistically more acts of aggression (22 and 27 acts, respectively) than did any of the other males or females. Additionally, *blue-right* and *yellow-right* received the fewest acts of aggression by other penguins (2 and 4 receipts, respectively). On the opposite end of the aggression was the juvenile penguin, initiator of 17 acts of aggression and recipient of 43 acts of aggression. Data in this case reveal a statistical bias in the rate at which the juvenile was attacked, making him the most deferent of the penguins.

Table 4: Aggression by Individuals

Individual	BR	PIR	JUV	YR	PuR	OR	GR	WL	RL	YL	BL	BkL	
Aggressor	22	10	17	27	14	12	6	4	6	6	4	1	129
Individual	BR	PIR	JUV	YR	PuR	OR	GR	WL	RL	YL	BL	BkL	
Recipient	2	11	43	4	9	13	7	5	7	11	7	6	125

Statistical analysis of the aggression by individuals (Table 5) reveals certain penguins as delivering statistically more acts of aggression and others as receiving statistically more of those acts of aggression. *Blue-right* and *yellow-right* (males) delivered higher numbers aggressive acts. Although *yellow-right's* rate of aggression is statistically significant, for the remainder of males, acts of aggression were not. Females in this study demonstrated fewer aggressive acts, but on a per individual basis, their low rate of aggression does not constitute significance. On the receiving side of aggression, *blue-right* and *yellow-right* were the objects of statistically few bouts of aggression while the remainder of the males and females (exception: *white-left*) gave statistically neutral results. The juvenile in this study was the object of 43 acts of aggression (χ square = 101.9). This accounts for approximately 1 of 3 acts of aggression (from both male and female) during the study. The juvenile also gave 17 acts of aggression, putting the juvenile on the high end of aggressiveness.

Table 5: Chi Square Values for Aggression

Aggressive Acts	BR	WL	GR	PiR	PuR	BkL	BL	YR	RL	YL	OR	Juv
χ square	11.77	4.24	2.098	0.05	0.98	8.84	4.24	24.56	2.098	2.098	0.145	3.63
Received Acts												
χ square	6.8	2.8	1.12	0.032	0.223	1.87	1.12	3.95	1.12	0.03	0.14	101.9

The females in this study show relatively lower rates of attack and were similarly the recipients of fewer attacks (Table 6). This information was considered in a dominance-deference assembly of individuals, but was not assessed as to whether the females were dominant or deferent to males. Females only initiated 18 directed acts at other individuals, while males initiated 111 attacks at other individuals (Table 6). Attacks by males were directed primarily at males, while attacks by females in this study showed no sex bias.

Table 6: Aggression Based on Sex

	MALE	Female	
Aggression			
Bill to Axilla	4	0	
Sideways Stare	10	1	
Alternate Stare	8	1	
Point	23	6	
Gape	9	0	
Peck	34	8	
Beaking	11	1	
Charge	8	1	
Attack	4	0	
TOTAL	111	18	129

Data also indicate that on a male and female basis, aggression of medium intensity (pointing, gaping and pecking) were most common - 59.5% (66 of 111) of male aggression and 77.8% (14 of 18) of female aggression.

A plot of aggressive acts over the three month period (Figure 1) reveals an initial peak of elevated aggression and a notable rise and a sustaining of this aggression over the period during which the three eggs were laid and the one recorded copulation occurred. The aggressive turns steadily declined after 17 March 1995 and maintained at approximately 5.17 aggressive acts per day until the termination of the study.

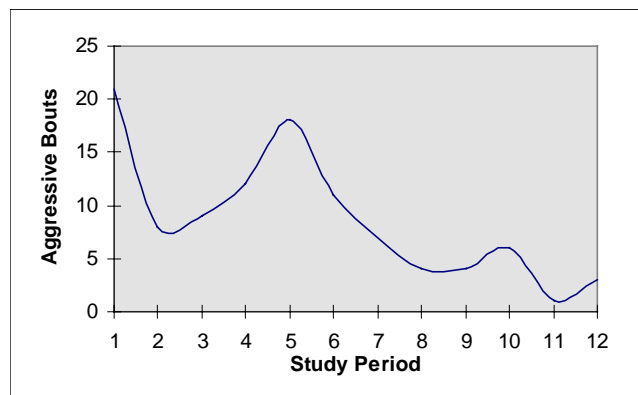


Figure 1: Aggression Over Time (4-7 = Egg Laying Window)

Pair Maintenance: Individuals were paired through the duration of the study as follows: *blue-right/white-left*, *yellow-right/blue-left*, *purple-right/black-left*, *green-right/pink-right*, and *yellow-*

left/red-left (Table 1). Over the three month period, extensive sexual displaying was observed in both males and in females. These observations recorded 9 different sexual displays of varied intensity and function (Table 7). The stable, unmated pair bond between *blue-right* and *white-left* exhibited 66 and 40 acts of sexual display, respectively. Other unstable, unmated pairs (the same sex female pair and male pair) showed higher than average (although not significant) displays between them. The stable and mated pairs demonstrated low rates of displays. Males in this study performed 74% (40 of 54) ecstatic displays while females gave 26% (14 of 54) ecstatic displays.

Table 7: Total Sexual Displays in Males and Females

Sex Display	BR	PiR	Juv	YR	PuR	OR	GR	WL	RL	YL	BL	BkL		TOTAL
Arms Act	0	2	0	1	1	0	0	0	1	0	0	0		5
Copulation	0	1	0	0	0	0	0	0	1	0	0	0		2
Ecstatic	19	6	0	0	0	6	4	0	7	5	0	0		47
Intent. Ecst.	2	0	0	0	3	0	0	0	2	0	0	0		7
Bow	2	3	1	0	4	0	1	1	3	2	4	0		21
Loud Mutual	19	0	0	0	0	0	6	18	3	5	0	2		53
Quit. Mutual	4	2	0	1	0	2	1	4	0	0	1	1		16
Trumpet	16	4	1	1	1	0	2	16	5	1	3	0		50
V. Head Mo.	4	5	2	3	6	4	2	1	3	1	0	0		31
TOTAL	66	23	4	6	15	12	16	40	25	14	8	3		232

Table 8 reveals the χ square data for significance of sexual displays and is arranged by pairs. For the unmated pair *blue-right* and *white-left*, the numbers of display on a per individual basis is significant (*blue-right* chi-square = 112.9, *white-left* chi-square = 22.1). Data concerning other paired individuals and unpaired individuals demonstrates statistically neutral or statistically insignificant values in support of the Richdale observations in Yellow-eyed and crested penguins. *Blue-right* maintained high rates of display, mated males (*purple-right* and *yellow-right*) maintained low rates or increased rates (*purple-right*) before and after pairing as did unpaired males orange right and same sex paired *pink-right* and *green-right*. (See figure 2 for graphical representation.)

Table 8: Chi Square Data for Total Sexual Displays (by Pairs)

Individual	BR	WL	GR	PiR	PuR	BkL	BL	YR	RL	YL	OR	Juv
χ Square	112.9	22.1	0.573	0.71	0.9699	13.7955	6.6489	9.19	1.66	1.47	2.77	9.19

Figure 2 demonstrates that varied sexual displaying occurred in males during the period of pair formation (exception: *green-right* and *pink-right* formed before observations). Graphical analysis confirms statistical interpretation of sexual displaying. Brief peaks at the end of the study in the display rates of *green-right*, *orange-right* and *purple-right* coupled with the same level of display in *yellow-right* fail to support completely the possibility of the Richdale observation being true in Humboldt penguins.

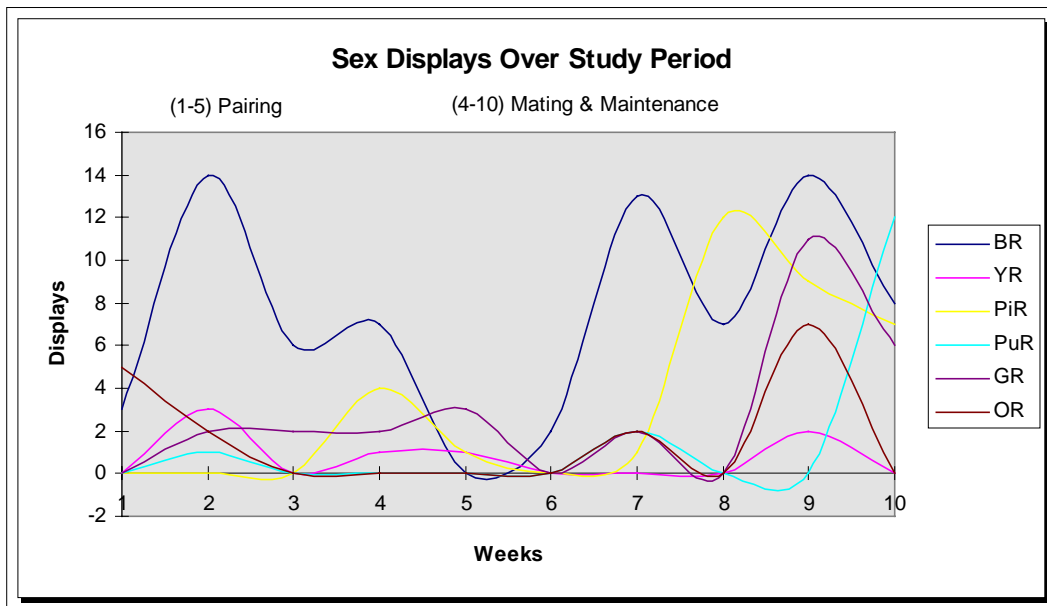


Figure 2: Sex Displays Over Study Period

Data does not support a relationship between numbers of sexual display and mating preference in females. *Orange-right* (unpaired) displayed more frequently (chi-square = 2.77) than did other mated *purple-right* and *yellow-right*, which each demonstrated neutral and low display rates (chi square = 0.9699 and low 9.19). *Blue-right* showed a statistically significant rate of display (chi-square = 112.9) but was not mated, although paired. *Green-right* and *pink-right* displayed at the same level as did *purple-right* but were both unpaired (sexually). *Red-left* and *yellow-left* chose to pair in the same sex bond and did not choose unpaired males, despite the fact that *pink-right* and *red-left* copulated once and displayed together on several occasions.

Social Integration of the Juvenile: As data in Tables 4 and 5 reveal, the juvenile penguin received statistically high amounts of the aggression exercised by other penguins. *Yellow-right* (the father; the mother of the juvenile was *brown-left*, deceased before study) acted aggressively toward the juvenile 5 times; these acts were of medium intensity and were not statistically differentiated from those attacks by others on the juvenile (Table 9).

Table 9: Aggression Towards Juvenile

<i>Aggressor</i>	BR	PiR	YR	PuR	OR	GR	WL	RL	YL	BL	BKL
<i>Attacks on Juvenile</i>	6	3	5	3	9	2	3	5	4	3	0
<i>χ Square Value</i>	1.64	0.09	0.563	0.09	8.2	0.7	0.09	0.563	0.049	0.09	0

This juvenile performed 4 sexual displays over the three months of record keeping. There was one act of submission (bowing, generally performed by females), one trumpet (performed with the father) and 2 vertical head movements (a typical male display). In the entire study males did not give statistically more vertical head movements than did females. The juvenile's rate of vertical head movement was not statistically important, and this display rate cannot be used as an indicator of sex at this time.

Throughout the duration of the study, the juvenile frequently engaged in recreational or "play" activity. This behaviour consisted of purpoising, tugging on the tails, flippers and feet of adult/subadult penguins, jumping on other penguins while in the water and swimming rapidly in circles. Seven of these acts provoked aggression in older penguins.

Foraging success was not affected by the statistical deference of the juvenile. The juvenile fed in the same manner as adults and frequently swam away from the feeding center to consume prey in the same manner.

DISCUSSION:

Aggression: Past behavioural theories have suggested that animals assess the value of resources and evaluate the costs and benefits of escalating competition when they are unsure of their opponent's likely response (Huxley, 1966; Lorenz, 1966; Smith, 1982). In this study an analysis of behaviours eliciting aggression demonstrates that aggression varied according to the value of the resource being contested. For the Humboldts, the likely resources were territorial space, food, nesting material, nesting space, and mates. In this study, data suggests the most highly valued resource was nesting space, nesting material and females, all three involving the same high level of aggression.

The varied aggression is best explained by the cost-benefit analysis or game theory animals may use when escalating contests into physical aggression. In this assessment, it is proposed that individuals weigh the cost and benefits of fighting. In incidents where proximity or passing by other penguins elicited aggression, threatening penguins employed low levels of aggression: visual displays such as bill-to-axillas, sideways stares and alternate stares. Presumably, the benefits of escalating this contest did not outweigh the costs of possible injury. Responses to these threats involved assessment on the same level but more often, the aggression was ignored and the bout ended.

When foraging, aggression was heightened. In this scenario, food became the defensible resource. Members of pairs often remained in nests throughout the day and relied on partners to return any food to the nest. In these situations (though attempts to feed all members were made by zoo keepers) competition for food was high and elicited physical aggression, primarily pecks, vocal warnings and when excessively close, beaking. During feeding times, aggression could be stimulated by walking up to the enclosure with a backpack extended at arms length. Arm movements were made to mimic feeding. These actions would drive penguins to the general locale where penguins would jockey for positions close to the wall. In this frenzy, pecking resulted. In all cases, recipients of pecks retreated in 2 of 3 (21 total) acts and in 1 of 3 (7 total) acts returned aggression on the same level. This level of aggression and its responses offers support to the cost-benefit analysis made by many animals and suggests that the benefits of

defending food or optimal foraging sites outweigh the costs of escalating this aggression: 1) acts of aggression for the first time became physical and 2) a higher percentage of responses were aggressive as well.

The highest level of aggression was employed to expel individuals from the nesting territory or from the close proximity to mates. Spurr (1975) demonstrated that Adelie penguins avoid conflict until resources such as nesting sites come into dispute, and it appears that Humboldts reserve high aggression for these situations as well. High level aggression (charging and attacking) results presumably in the most injury; however, we presume the loss of genetic fitness to be a cost of not defending this resource. Presumably the cost of losing fitness is greater than the cost of injury in this situation. In this study, violations of nesting territory and mate disturbance provoked attack and resulted in the sometimes noisy retreats of the intruder. Winners were in all cases associated with the territory, as in Adelie penguins (Spurr 1975). The "homefield advantage" may have some effect in who wins territorial disputes since the holder has more to lose by not defending (Krebs & Davies, 1993). To test this homefield advantage, Humboldt penguins would need to be switched to another environment and allowed to contest new territories. As of date, no similar study has been made of any penguin species.

One method of testing these assumptions is to offer penguins optimal nesting sites, complete with the necessary implements for constructing those nests, geographically place nests close to food sources. To assess whether cost-benefit analysis is being requires placing penguins in this locale where optimal nests and suboptimal nests are provided. It is to be assumed that the owner of the nest would always defend this area and if two penguins unfamiliar with each other are allowed to contest an unowned, optimal site, we would expect to see more visual displays in order to confirm the Maynard Smith theory.

To demonstrate the serious nature of these resources, *green-right* on more than one occasion left his nesting cove to steal nest material from the nesting cove of *yellow-right* and *blue-left*. After 5 or 6 trips back to his nest, *yellow-right* who was swimming caught sight of *green-right*, left the pool, ran approximately 3 meters and repetitively thrashed *green-right* with his flippers while pecking *green-right* on the back of the head and neck. This battle was markedly loud, given

green-right's cries and *yellow-right's* growling threats. In yet another incident, *blue-right* peered in to the nest of *purple-right* and *black-left*. Instantly *purple-right* launched out of his nesting cove and jumped onto *blue-right* while beating his flippers and pecking indiscriminately until *blue-right* retreated to the water. Other incidents of attack were less dramatic; however, they all were provoked by an individual who loitered around a nesting cove or interfered with a mate by giving vertical head displays. Cost-benefit analysis predicts this level of aggression over a resource as highly valued as nesting sites, nesting material and mates. A comparison with other colonial avian species reveals similar levels of aggression. White-fronted bee eaters (*Merops bullockoides*) lives in colonies and battles regarding intra-specific nest parasitism and invasion are particularly intense while territorial invasions are first countered with viscous chatter. Females have been observed to battle over nesting sites for 2 or more hours until the point of exhaustion (Emlen, 1984). For emperor penguins, Joventin (1982) observed that battles over nesting territories generate such aggression that occasionally parents attacked their own chicks while expelling intruders. The battle for abandoned chicks is equally physical and more often results in high chick mortality.

The question that rises in this situation regards which resource is being more heavily defended. The Humboldts may be defending the females or they may be defending the nesting sites (or both). Observations from this study suggest both occur. Birkhead and Møller (1992) suggest in the sperm competition hypothesis that in colonial species, high levels of mate defense occur over the period of receptivity in females. This assumption is supported by data (Figure 1) that reveal an increase in the aggressive acts during the window in which eggs were laid. Data is further supported by the Tinbergen (1939) observations that fighting occurs before and during pair formation of bonds. For the Humboldt penguins, this is not simply a rise in aggression, but a rise involving all but one of the high level acts of aggression (charges and attacks) employed by *yellow-right* and *purple-right*. Richdale (1951) claims that aggression in Yellow-eyed penguins has a pair formation value, is involved in mate defense or has territorial significance. The latter two may be seen in the Humboldts. Since territories seem to be limited to the nesting area, mate defense may also include nest defense. Gulls, herons and Yellow-eyed penguins defend nesting

grounds only (Richdale 1951) and nesting territory defense appears to be true of the Humboldts. However, aggression over nesting territories need not involve mates.

The aggression over mates, according to Davis (1940, 1941, 1942), does not necessarily equate to fighting over territories, and observations from this study tend to support this assumption since *pink-right*, in a same-sex bond, defended his nest with as much fervor as did mated males.

Richdale (1951) also observed that once eggs were laid, rivalry amongst penguins was not a "concern." His claim was that the social bond could not be broken at this point and that the risk of cuckoldry was low. As they related to aggression, there is no evidence for this assumption in the Humboldts. Aggression did decrease after egg laying; however, this was due by and large to the fact that pairs spent a great deal of time in the nesting coves and exited only to feed or swim. Little interaction was observed after the 9th week of observation.

Although mates were defended heavily, the nesting ground was defended more frequently. This does not negate the possibility that males employ means to avoid cuckoldry, rather the contents of the nest seem more important and more frequently contested. To test these assumptions as being *evidence* in support of cost-benefit analysis requires a test to see if unpaired males with nest sites defend this area with as much energy as do paired males on nesting sites. The defense of nest #4 by *pink-right* offers some evidence to this effect.

Binary Aggression: With the exception of two acts of nest defense and beaking, all acts involving fighting were terminated after two turns. Targets of aggression either fought back or did not return aggression; in either situation, the original aggressor did not escalate the contest further. These observations allow the data to be placed in a table (Table 3) which established a binary system of interaction in these Humboldt penguins. The binary system of aggression allows us to view the cost-benefit analysis from another perspective. The resource cannot be determined from this table of data; however, the data reveal that acts of aggression more often were responded to with "retreats" and "no responses" than they were with aggressive acts. In the 24 cases in which aggression was the response, at no time was the aggressive response an act

of greater intensity than that of the initiator. The sum of all data demonstrates that as aggression intensified, the more likely the response was to be a "retreat" or a "no response." The least intense actions (bill-to-axilla, sideways stare and alternate stare) were largely ignored by targets; 13 of 20 cases, 65% were "no response" actions. In 15% of the cases (3 of 20), a penguin retreated. Aggression of medium intensity (point, gape) resulted in a higher percentage of retreats. In 33 of 65 events of the cases (48.6%) of medium aggression, penguins resorted to retreating, and fewer responses to this aggression involved "no response" (26.2% or 17 of 65 cases). In all 13 cases of high intensity aggression (charge, attack) the response was an obvious a "retreat."

The increasing percentages of retreat correspond with the heightened level of aggression. As aggression intensifies, the percentage of retreats increases. This can be viewed as avoiding aggression. These observations at least suggest that the Huxley/Lorenz propositions and the Maynard Smith hypothesis are being supported by observations from the Humboldt penguins.

In summary, as aggression itself intensifies, the less likely a penguin is to escalate that aggression or respond on the same level of aggression. There is a caveat to this discovery, however. When this data is analyzed with data concerning the causes of aggression, we see that as the value of the resource increases, the likelihood that a penguin will defend that resource increases. These observations reveal that this group of penguins may be acting to minimize aggression, but can only be tested by providing certain penguins with differential resources. This will permit experimenters to assess the true responses to aggression under limited resources.

Dominance: In his study of Gentoo penguins, Roberts (1940) determined the male to be dominant over the female. The yellow-eyed penguins in Richdale's (1951) study showed no such bias. The data in this study regarding the dominance by one sex is inconclusive. Males were more aggressive than females; however, males directed aggression primarily at other males while females showed no bias in directed aggression. No sex dominance was observed in these Humboldt penguins.

Within sexes, no female revealed herself as statistically more aggressive than any other female. For the males, *blue-right* and *yellow-right* were numerically more aggressive than other males. Although *yellow-right* was statistically more aggressive, *blue-right*'s aggression was only of moderate significance.

Rate of aggression is poor criterion for establishing dominance; however, when coupled with the rate at which the individual is attacked, the issue of dominance becomes clearer. Regarding dominance, Nice (1943) addressed three issues: *supersedence* - the ability to displace another individual, *peck-dominance* - based on who wins more fights and *peck-right* - a rigid order and independent of place. Richdale (1951) found no support for the latter two qualifications, and support for only the second qualification was observed in this study. Individuals avoided aggression by bowing and by employing the slender walk (Spurr, 1975), but these acts were not labeled as deferent acts since all penguins used these avoidance techniques. At no time was an individual observed to supersede another individual.

The data collected in this observation suggest that we cannot arrange the Humboldts into a dominance hierarchy, at least not a hierarchy that requires Nice's (1943) three qualifications. The only male to demonstrate aggression of high statistical relevance was *yellow-right*. *Yellow-right* was not observed to attack *blue-right*, nor was the converse true. *Yellow-right*, however, was engaged 4 times while *blue-right* was engaged 2 times; this difference does not hold any significance. From the information, we can conclude only that *yellow-right* was statistically the most aggressive. Thus, if Nice's peck-dominance were accurate enough for establishing dominance, *yellow-right* would be dominant; however, *yellow-right* was never observed to supersede another individual. One true mark of dominance is the immediate right to a resource, the ability to displace another individual (supersede). This was not observed in any member of the Humboldt group.

The Richdale Observation: In his 1951 report on the Yellow-eyed and crested penguins, Richdale observed that the mated birds did not engage in what he calls the more serious "love habits." By definition, Richdale refers to all variations on the ecstatic display (and other high

visibility ante-nuptial displays). Richdale claims that this behaviour was restricted to the “unemployed” - any bird, regardless of paired status, that was not tending to eggs.

To see if this observation was true of the Humboldt penguins, sexual displays were observed over a 10 week period. During this period, pairs were formed and in two pairs, eggs were laid. Tables 7&8 and Figure 2 amalgamates information on the incidence of sexual display in individuals. To confirm the Richdale observation, the rate of sexual advertising must *decrease* in mated pairs and remain constant or increase in unmated individuals. Since *green-right* and *pink-right* were paired before observations were made, whether their low rates of display decreased is unknown; however, since both members of this pair were male, they were not considered to be successfully paired.

Specifically, the numbers of display in *purple-right* and *yellow-right* must decrease. In fact they did not. Rate of sexual display in *yellow-right* was constant as was for *purple-right* until the last weeks when his displaying increased. A successfully paired (not mated) male, *blue-right* did demonstrate Richdale’s observation since his rate of display remained constant throughout. *Orange-right* decreased in rate after the first two weeks and increased briefly during the last three weeks.

In retrospect, the only evidence in support of Richdale’s observations seems to be that of *blue-right*. This high rate of display may be due to several factors, including the Richdale observation. *Blue-right* appeared to be particularly “androgenic,” given his statistically high rate of aggression and moderately high level of aggression. We expected the rates of display in *yellow-right* and *purple-right* to decrease; they did not. Additionally, the data for *orange-right* does not conform to any standard. The sum of all data does not lend support to the possibility of the Richdale observation being true in this group of Humboldt penguins.

In any event, the Richdale observations cannot be entirely discounted either. Problems generally arise when sample sizes are small. Richdale dealt with several hundred birds over a 9 year period while this study involved 12 birds during 12 weeks. One way to confirm or deny this conclusion is to test the Humboldts over the 2 breeding windows during the calendar year.

Sexual Attractiveness of the Ecstatic Display: The ecstatic display is visually the most dramatic and potentially most exhausting sexual display in penguins. Ecstatic displays may be provoked by the absence of mates (Ainley, 1975), by the ecstatic displays of other males (Spurr, 1975) or be initiated without provocation. This display is given chiefly by males (Ainley, 1975) and begins with the focal penguin taking several deep breaths of air. The penguin subsequently points his bill to the sky and emits a harsh braying sound. The vocalization is coupled with the arching of the flippers as far back as possible. The chest caves in upon emission and there may be up to 5 iterations of this activity while the head may bob up and down. The penguin may follow up with another ecstatic display, but typically the penguin rests. The ecstatic display is broken into 3 levels of intensity: the intention ecstatic (an incomplete ecstatic display), the normal ecstatic and the imploring ecstatic (marked by particular excitement and/or duration).

In this study, there were 54 ecstatic displays (normal and intention), half by *blue-right* (21 acts). It was supposed that the ecstatic display, given its high visibility and volume, might be an indicator of male strength or androgenic state and relate to female choice. As results indicated, this assumption was not supported.

As Table 7 reveals, successfully mated males (*purple-right* and *yellow-right*) gave the *fewest* ecstatic displays. All unpaired males displayed with higher frequency than did these males, while paired but unmated *blue-right* displayed with the highest frequency. While the data does not support the hypothesis, it does not detract from it either. As suspected, there may be other forces which influence female choice. The ecstatic display may be an honest indicator of health and ability; however, females may not use this as the principal determining factor in choosing a mate.

One problem was considered in this analysis - the possibility that the ecstatic display supported the Richdale observations. This would make the ecstatic display the confounding variable in the Richdale and sexual attractiveness tests. As part of the Richdale observations, the ecstatic display may have been used profusely before pairing occurred, i.e. before the initial weeks of the study, and subsequently died off in successfully mated males. Thus, the ecstatic display may have been the determining factor for *yellow-right* and *purple-right*, but after they were

paired and mated, these “love habits” decreased. Again, we must consider the observation period. Ecstatic displays may have been given during hours when observation was not possible.

Since nest resources and food resources were never unpredictable, it is unlikely that these two factors played large roles in mate selection, though this could have been tested experimentally. Possible factors involved in choice may have include fighting ability. *Blue-right* and *yellow-right* stand out as the most aggressive. Of other interest is *orange-right*, whose left flipper was amputated. It is possible that this handicap put him at a disadvantage in competition, foraging and displaying - perhaps the ecstatic display is more of a visual display than it is a vocal display. There may also be another explanation for this lack of concordance: Humboldts are monogamous and faithful over subsequent seasons (Murphy, 1936). Perhaps mated individuals in this study mated previously in the winter or summer.

More study is required to assess the role of the ecstatic display in Humboldts. As far as the assumption is related to any data provided in this study, the ecstatic display cannot be used to predict male preference in females. However, to offer up evidence in support of the original assumption requires playback experiments - to see if the ecstatic display is a vocal display - or exogenous treatment of hormones to subordinate males. It is likely that many more factors are involved in female choice. These factors were not tested or assumed herein.

Social Integration of the Juvenile: The juvenile penguin, 11 months by study's end, was the target of statistically more aggression than any other individual; while there is no evidence for age ordered dominance (there is weak evidence for a peck-dominance), the juvenile clearly ranks last among the penguins. The juvenile exhibited a higher than average rate of aggression; however, most of these acts were in retaliation and did not initiate bouts of aggression. No particular penguin stood out as being statistically more aggressive towards the juvenile.

When a penguin cannot be sexed invasively, behavioural clues are the other alternative to determining sex. This method is not nearly as reliable; however, in a species such as the Humboldt penguins where displays such as the ecstatic display have sexual bias, behavioural sexing can be an alternative. The juvenile gave 4 sexual displays. Only 2 of them potentially

carry information regarding sex. In the crested penguins (Warham, 1975), the vertical head sway is typically a male display as is in the Galapagos penguins (Mills, personal communication). The vertical head sway is slightly modified in *Spheniscus*, the vertical head "movement" (Welch, 1994). However, in this study there was no statistical bias in which sex gave the display. Hence, this display cannot be used to sex the juvenile penguin.

Play is widely documented in animals and especially in penguins. Richdale (1951) states that behaviour of any nature has either a social value or a sexual value, so play may be regarded as having social value. For juveniles, play may be a means of developing social "skills." Spurr (1975) and Ainley (1975) document cases of Adelie penguins locomoting in social groups, hopping onto ice floes, riding those floes down current, hopping off and repeating the trip on another ice floe. This behaviour seems to serve no function other than recreation, so whether play has to have what Richdale determines to be a social value is undetermined; however, for the juvenile Humboldt penguin, play may indeed have a social value. Of particular notability were the play acts that elicited aggression. The juvenile frequently tugged on the various appendages of adults throughout the study. In one incident, this resulted in what may be considered as playful chase, marked by extensive purposing and swimming around in circles. In 7 other cases, the play provoked aggression, i.e. pecking. In one other incident, the juvenile, after foraging, swam a few meters away from the pack to "play" with his food. The juvenile nibbled on the fish, threw it around and exhibited behaviour which was likened to the hunting methods - hovering below the fish and darting up to prey upon it. This behaviour only resulted in *red-left's* stealing of the fish.

CONCLUSIONS: From observations, we come to three principal conclusions: 1) aggression in this group of Humboldt penguins is caused by five behaviours and each of these behaviours elicits a varied intensity of aggression. The level of aggression corresponds to the value of the resource. Aggression is an expensive means of assessment and is minimized to one bout; 2) sexual displays do not show the downward trend in frequency as seen in Richdale's (1951) study. The ecstatic display, though highly visible and energetic, cannot be used to predict female preference; 3) the juvenile penguin was the most deferent individual in the group. Lack of sexual display and

lack of sexual bias in those sexual displays tested do not permit the behavioural sexing of this bird. These observations are not supported by experimental evidence.

APPENDIX

Chi-Square data for 11 degrees of freedom:

0.995	0.99	0.975	0.95	0.90	0.75	0.50	0.25	0.10	0.05	0.025	0.01
2.60	3.05	3.82	4.57	5.58	7.58	10.3	13.7	17.3	19.7	21.9	24.7

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