GENETIC EVIDENCE FOR LOW FREQUENCY OF EXTRA-PAIR FERTILIZATIONS IN NORTHERN GOSHAWKS[1]

THOMAS A. GAVIN

Department of Natural Resources, Cornell University, Ithaca, NY 14853,
e-mail: tag1@cornell.edu

RICHARD T. REYNOLDS, SUZANNE M. JOY AND DOUGLAS LESLIE[2]
Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, 3825 E. Mulberry,
Ft. Collins, CO 80524

BERNIE MAY[3]
Department of Natural Resources, Cornell University, Ithaca, NY 14853

Abstract.   We collected blood for allozyme analysis from Northern Goshawks (*Accipiter gentilis atricapillus*) on the Kaibab Plateau in northern Arizona during 1991–1993 to quantify frequency of extra-pair fertilizations (EPFs). Northern Goshawks are socially monogamous, territorial, noncolonial, synchronous breeders, and their nests are relatively far apart, characteristics that suggest that EPFs should be low. We sampled 103 adults and 122 nestlings from 64 nests. Both putative parents were sampled at 39 nests, but we were able to capture and sample only one putative parent at 25 other nests (84%, female only; 16%, male only). Of the 39 complete families sampled, only 1 of 77 (1.3%) nestlings (or in 1 of 39 clutches, 2.6%) had a genotype not consistent with both parents; the male was excluded as the genetic father of this nestling. When this estimate was adjusted based upon the probability of excluding a putative father when he is not the actual father, the estimate of nestlings sired by EPFs was 9.4% in 1991 and zero in 1992 and 1993. There was no evidence of egg-dumping. Our data suggest that EPFs are infrequent in Northern Goshawks breeding in northern Arizona, a result consistent with characteristics of their mating system.

Key words: Accipiter gentilis, allozymes, EPCs, EPFs, Northern Goshawk.

Many raptors have a division of sex roles during the active breeding period. In species that demonstrate reverse sexual-size dimorphism, the males forage and provision females and offspring with prey, whereas females incubate and brood offspring at nests (Brown and Amadon 1968, Reynolds 1972, Newton 1979). Sex-role differences are first evident during courtship when the male spends much of the diurnal period in

search of food for his mate at long distances from the nest in forests, where he cannot maintain visual contact with the female. Between courtship feedings, females are quiescent in nest areas while storing energy for the production of their clutches. During the fertile period before and during egg laying, females are alone at nests while their mates forage. Because visits to nests by conspecific males and extra-pair copulations (EPCs) occur during this period in raptors (Birkhead and Lessels 1988, Reynolds and Linkhart 1990, Negro et al. 1992), there is a risk of extra-pair fertilizations (EPFs). Among males, whose investment in a breeding attempt is the long-term provisioning of their mates and offspring, natural selection would favor behaviors that minimize EPFs and, therefore, increase the male's assurance of paternity.

In Europe, male Northern Goshawks (*Accipiter gentilis gentilis*) guard against EPFs by maximizing time spent with their female during the fertile period and copulating at a high rate—as many as 500–600 copulations per clutch (Holstein 1942, Møller 1987). Presumably, male attendance of females reduces risks that females will be visited by other males for EPCs, and frequent copulations increase a male's probability of paternity because the chances of fertilization increase with the number of copulations and decrease with age of sperm (Lodge et al. 1971, Martin et al. 1974, Birkhead and Lessels 1988).

Although EPCs have not been observed in Northern Goshawks in either North America or Europe, EPCs have been observed in other raptors. Here we present genetic evidence that supports the rarity of EPFs in a large and relatively dense population of Northern Goshawks (*A. g. atricapillus*) in northern Arizona.

METHODS

The study area encompasses the coniferous forests > 2,134 m elevation on the Kaibab Plateau in northern Arizona, an oval-shaped (95 × 55 km), limestone plateau that rises from a shrub-steppe plain (1,750 m) to spruce (*Picea*)/fir (*Abies*) forests at 2,800 m (Rasmussen 1941). Total area covered by forests on the plateau, which include the Grand Canyon National Park and North Kaibab Ranger District, is about 3,206 km². For-

est types include pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands, ponderosa pine (*Pinus ponderosa*) forests, and mixed-conifer forests (*P. ponderosa, Abies concolor, Pseudostuga menziesii, Picea engelmannii*, and *Populus tremuloides*) (Rasmussen 1941).

We initiated systematic searches for nests of Northern Goshawks on the Kaibab Plateau in 1991 using methods described in Reynolds (1982) and Joy et al. (1994). In subsequent years (1992–1995) we expanded the area searched; in 1996 ~90% of the plateau was searched for Northern Goshawk nests. A total of 107 Northern Goshawk territories (an area used exclusively by a pair of banded hawks from year to year) was located that had active nests (contained eggs) (103 territories) in one or more years or were occupied by nonbreeding hawks (4 territories). Not all territories were occupied by Northern Goshawks every year; annual occupancy varied from a high of 91% (61 of 64 territories) in 1992 to a low of 23% (19 of 82 territories) in 1994. In 1992, territories were dispersed on the plateau at a mean (± SD) distance of 3.0 ± 0.8 km based upon 59 nearest-neighbor active nests (Reynolds et al. 1994). Thus, the density of nests on the Kaibab Plateau (about 8 breeding pairs 100-km^{-2}) is higher than reported for any other Northern Goshawk population in North America.

Adult hawks were captured in their nest areas during the nestling and fledgling stages with either dho-gaza traps using a live Great Horned Owl (*Bubo virginianus*) (Bloom 1987) or "falling-end" Swedish Goshawk traps (Kenward and Marcström 1983) baited with domestic pigeons (*Columba livia*). All adult goshawks were fitted with color-bands and a USFWS aluminum band. The age (subadult, adult) and sex of trapped birds were determined by plumage, mass, and tarsus length. During the fourth and fifth weeks of the nestling period, we climbed nest trees and lowered nestlings to the ground to be measured and banded (Reynolds et al. 1994). About 0.2 cc of blood was collected from the brachial vein of each Northern Goshawk, sealed in a cryogenic tube, and stored in liquid nitrogen for < 4 months. Twenty-one loci known to exhibit variation in other avian species were assayed using starch-gel allozyme electrophoresis (May 1992). All samples were scored in the lab by personnel who had no knowledge of putative relationships among the individual birds.

Allelic frequencies were summarized and heterozygosities and Hardy-Weinberg deviations were calculated using the program "Genes in Populations" (available at http://animalscience.ucdavis.edu/extension/gene.htm). Paternity exclusion analysis involves determining whether the genotype of the putative father is consistent with the genotypes of the nestlings, assuming no intraspecific nest parasitism, or "egg dumping." However, two males may have genotypes comprised of the same alleles, so that either could be the genetic father of a nestling. This results in relatively low power to detect a nestling not sired by the male in attendance at that nest if, in fact, that male was not the genetic father. Westneat et al. (1987) developed a technique for calculating the probability of excluding a putative father when he is not the actual father, assuming the female at the nest is the actual mother (the EPC

TABLE 1. Frequencies of alleles at the Np locus in 162 Northern Goshawk adults in Arizona during 1991–1993.

Allele	1991 ($n = 43$)	1992 ($n = 62$)	1993 ($n = 57$)
1	0.430	0.452	0.404
2	0.081	0.089	0.061
3	0.349	0.338	0.360
4	0.128	0.097	0.149
5	0.012	0.024	0.026

case). A general equation for loci with multiple alleles to calculate the probability of detection (d) of non-kin was developed by Chakravarti and Li (1983): $d = 1 - 2a_2 + a_3 + 3(a_2a_3 - a_5) - 2(a_2{}^2 - a_4)$, where $a_n = \sum_{i=1}^{k} p_i{}^n$, p_i is the frequency of the ith allele, and k is the number of alleles. We calculated d for each of the three years using the total sample of adults captured each year (from Table 1). The observed number of exclusions can then be divided by this probability to obtain an estimate of the actual number of exclusions. There is no comparable general equation for calculating the probability of detecting egg-dumping at a locus with more than two alleles, under the assumption that egg-dumping is the only cause of stray genes (Westneat et al. 1987).

We used allozyme markers for this study because this parentage study was initiated after we had already chosen allozymes and single-locus microsatellite markers for an analysis of differentiation among Northern Goshawk populations in North America. Microsatellite markers, which are more expensive to produce, were no more variable than the allozyme markers.

RESULTS

A total of 43 adult males, 60 adult females, and 122 nestlings from 64 nests (= families) was sampled and analyzed for allozyme variation from 1991 to 1993. We sampled both putative parents at 39 nests ($\bar{x} = 2.0$ nestlings per nest), but we were able to capture and sample only one putative parent at 25 nests (21 nests with female only and 4 nests with male only). Nineteen loci were monomorphic in an initial examination of 38 adult Northern Goshawks (Aat, Ak-1, Ak-2, Ck, Gpi, Hb, Idh, Mdh-1, Mdh-2, Mpi, Pep-GL, Pep-PAP, Pgd, Pgm-1, Pgm-2, Pro-1, Pro-3, Sod, and Tpi), and two loci were polymorphic (Pp [inorganic pyrophosphatase], E.C.# 3.6.1.1; and Np [nucleoside phosphorylase], E.C.# 2.4.2.1). Pp could not be reliably scored, leaving Np as the only usable locus; Np had five alleles segregating. Frequency of these alleles did not differ (*G*-test; $G_{10} = 3.0$, $P > 0.97$) among years for 162 adults sampled (Table 1), which included an additional 59 adults not analyzed for paternity because their nestlings were lost before sampling. Observed heterozygosity at Np ranged from 0.628 (1991) to 0.702 (1993). In no year did the genotypic frequencies deviate from Hardy-Weinberg expectations, suggesting that mating was random in this population, and that mutation and selection were negligible with respect to the genes at the Np locus.

Of the 39 families where both putative parents and > 1 nestling were sampled, the genotype of only one nestling was not consistent with both parents (adult male = homozygous for allele "1," adult female = homozygous for allele "3," nestling = heterozygous, and exhibited alleles "2" and "3"). Based upon these data we excluded the male as the genetic father of this nestling, which was the only nestling in this 1991 nest. Only 1 of 15 nests in 1991 ($n = 26$ nestlings; $d = 0.409$) and none of the nests sampled in 1992 ($n = 8$ clutches, 19 nestlings; $d = 0.407$) or 1993 ($n = 16$ clutches, 32 nestlings; $d = 0.423$) contained a nestling where the putative father was excluded as the actual father. Therefore, in only 2.6% (1 of 39) of clutches did we observe a nestling that was apparently sired by an EPF.

The observed percentage of extra-pair paternity-offspring (sensu Birkhead and Møller 1992) was 3.9% in 1991, 0% in 1992, and 0% in 1993, or 1.3% (1 of 77 nestlings) for all years combined. Therefore, the estimate of nestlings sired by EPCs becomes 1 observed nestling/$d = 0.409$, which equals 2.45 nestlings or 9.4% in 1991. Estimates for 1992 (0/0.407) and 1993 (0/0.423) are zero, because in each year there was no observed exclusion.

Of the 60 nests where we sampled the female and male, or only the female, no nestling ($n = 115$) had a genotype that was inconsistent with the female in attendance at that nest. More than one female was never observed (e.g., when trapping in the nest area) to be active at the same nest and there were no observations of helpers-at-the-nest in any Northern Goshawk territory.

Territory #19 in 1991, which contained the nest at which we documented the EPF, was contiguous with at least five territories containing active Northern Goshawk nests; all were 2.5–6.4 km from the nest in territory #19. The uncommon "2" allele (frequency of 8.1% in 1991) was not found in any of the adults sampled on contiguous territories, although this allele was more frequent in adults resident in this region (north end) of the plateau than in those farther south. Both Northern Goshawks trapped at territory #19 in 1991 were adults. It was not known how many years prior to 1991 this pair nested on this territory, and these adults were replaced by a new male and female in 1992.

DISCUSSION

Our allozyme data indicated that EPFs in Northern Goshawks on the Kaibab Plateau were infrequent (mean of estimated proportion of exclusions, all years combined = 3.1% of nestlings). Although few genetic data on extra-pair paternity in raptors are available, our result is consistent with the low estimated percentage of extra-pair paternity-offspring in hawks, 5.4% in *Accipiter nisus* (Birkhead and Møller 1992), 0.0% in *Falco columbarius* (Warkentin et al. 1994), 3.4% in *Falco naumanni* (Negro et al. 1996), and 1.9% in *Falco tinnunculus* (Korpimäki et al. 1996). Faaborg et al. (1995) found that 5 of 6 two-chick broods in Galapagos Hawks (*Buteo galapagoensis*) were multiply sired, but in this species each breeding group is comprised

of one female and 2–8 males (i.e., cooperative polyandry).

One strategy for paternity assurance is for the male to copulate frequently with the female on his visits to the nest (i.e., provisioning of prey) during her fertile period (Møller and Birkhead 1991). A high copulation rate may result in more sperm placed in the female and, therefore, a higher probability that his sperm will fertilize eggs even if EPCs have occurred, and a higher probability that he will have been the last male with which the female copulated, because the last copulation is more likely to provide the sperm for fertilizing the next egg in birds generally (Birkhead and Møller 1992, Briskie 1996). In addition, if females are so dependent on foraging males during the egg-laying and brooding periods, females may use the male's provisioning rate (along with other measures of male quality) to "decide" whether to participate in EPCs. Alternatively, low EPF rates may indicate that engaging in such behavior may be costly to both sexes (Lawless et al. 1997).

Northern Goshawks in Europe have one of the highest copulation rates of any bird, a mean of 518 per clutch (Møller 1987), but there are no published data on copulation rates in Northern Goshawk populations in North America. We hypothesize that copulation rates are high in Northern Goshawks to increase assurance of paternity, given that males spend less than 20% of daylight hours in the nest area (Reynolds, pers. observ.). A testable hypothesis is that there is an inverse relationship between copulation rates and time spent guarding the female. If Northern Goshawk prey were abundant in some years or geographic areas, males might spend less time away from their nest and, therefore, copulate less than males that spend more time away from their mate. Similarly, Sharp-shinned Hawk (*A. striatus*) and Cooper's Hawk (*A. cooperi*) males capture smaller prey (Storer 1966, Reynolds and Meslow 1984) and make more frequent prey deliveries to the nest and, therefore, can presumably spend more time guarding mates. More frequent guarding provides greater assurance of paternity and, perhaps, results in less frequent copulations in these smaller congeners than in Northern Goshawks.

Northern Goshawks on the Kaibab Plateau are socially monogamous, territorial, and noncolonial, and breeding is synchronous (i.e., all eggs laid within a 2–3 week period). Westneat et al. (1990) and Møller and Birkhead (1993) predicted that these mating system characteristics would result in a low frequency of EPFs, which is consistent with our results. In addition, density of Northern Goshawks on the Kaibab Plateau is the highest reported for this species in North America. Westneat and Sherman (1997) reviewed the relationship between density and EPFs in birds and concluded that within a species, EPFs appeared to increase with density. High density should increase encounter rates between females and neighboring males and, perhaps, lead to greater EPC rates. These rates may be offset somewhat, however, by the absolute distance between nests in Northern Goshawks, which is at least several kilometers. We conclude that the high copulation rate presumed for North American Northern Goshawks, based on observations of this same species in

Europe, further reduces the probability that an EPC will result in an EPF. The low frequency of EPFs that we documented for this relatively dense population suggests that EPFs should be even lower in other populations of this species.

LITERATURE CITED

BIRKHEAD, T. R., AND C. M. LESSELS. 1988. Copulation behavior of the Osprey *Pandion haliaetus*. Anim. Behav. 36:1672–1682.

BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds. Academic Press, London.

BLOOM, P. H. 1987. Capturing and handling raptors, p. 93–123. *In* B. A. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [eds.], Raptor management techniques manual. Natl. Wildl. Fed. Sci. Tech. Ser. No. 10.

BRISKIE, J. V. 1996. Spatiotemporal patterns of sperm storage and last-male sperm precedence in birds. Funct. Ecol. 10:375–383.

BROWN, L., AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill, New York.

CHAKRAVARTI, A., AND C. C. LI. 1983. The effect of linkage on paternity calculations, p. 411–420. *In* R. H. Walker [ed.], Inclusion probabilities in parentage testing. Am. Assoc. Blood Banks, Arlington, VA.

FAABORG, J., P. G. PARKER, L. DELAY, TJ. DE VRIES, J. C. BEDNARZ, S. M. PAZ, J. NARANJO, AND T. A. WAITE. 1995. Confirmation of cooperative polyandry in the Galapagos Hawk (*Buteo galapagoensis*). Behav. Ecol. Sociobiol. 36:83–90.

HOLSTEIN, V. 1942. Duehøgen. Hirschsprung, Copenhagen.

JOY, S. M., R. T. REYNOLDS, AND D. G. LESLIE. 1994. Northern Goshawk broadcast surveys: hawk response variables and survey costs. Stud. Avian Biol. 16:24–31.

KENWARD, R. E., AND V. MARCSTRÖM. 1983. The price of success in Goshawk trapping. Raptor Res. 17: 84–91.

KORPIMÄKI, E., K. LAHTI, C. A. MAY, D. T. PARKIN, G. B. POWELL, P. TOLONEN, AND J. H. WETTON. 1996. Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. Anim. Behav. 51:945–955.

LAWLESS, S., G. RITCHISON, P. H. KLATT, AND D. F. WESTNEAT. 1997. The mating strategies of Eastern Screech-Owls: a genetic analysis. Condor 99: 213–217.

LODGE, J. R., N. S. FECHEIMER, AND R. G. JAAP. 1971. The relationship on in vivo sperm storage interval to fertility and embryonic survival in the chicken. Biol. Reprod. 5:252–257.

MARTIN, P. A., T. J. REIMERS, J. R. LODGE, AND P. J. DZUIK. 1974. The effect of ratios and numbers of spermatozoa mixed from two males on the proportion of offspring. J. Reprod. Fert. 39:251–258.

MAY, B. 1992. Starch gel electrophoresis of allozymes, p. 1–27. *In* A. R. Hoelzel [ed.], Molecular genetic analysis of populations. IRL Press, New York.

MØLLER, A. P. 1987. Copulation behaviour of the Goshawk, *Accipiter gentilis*. Anim. Behav. 35:755–763.

MØLLER, A. P., AND T. R. BIRKHEAD. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. Behaviour 118:170–186.

MØLLER, A. P., AND T. R. BIRKHEAD. 1993. Cuckoldry and sociality: a comparative study of birds. Am. Nat. 142:118–140.

NEGRO, J. J., J. A. DONÁZAR, AND F. HIRALDO. 1992. Copulatory behaviour in a colony of Lesser Kestrels: sperm competition and mixed reproductive strategies. Anim. Behav. 43:921–930.

NEGRO, J. J., M. VILLARROEL, J. L. TELLA, U. KUHNLEIN, F. HIRALDO, J. A. DONÁZAR, AND D. M. BIRD. 1996. DNA fingerprinting reveals a low incidence of extra-pair fertilizations in the Lesser Kestrel. Anim. Behav. 51:935–943.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

RASMUSSEN, D. I. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11:230–275.

REYNOLDS, R. T. 1972. Sexual size dimorphism in accipiter hawks: a new hypothesis. Condor 74:191–197.

REYNOLDS, R. T. 1982. North American accipiter hawks, p. 288–289. *In* D. E. Davis [ed.], Handbook of census methods for terrestrial vertebrates. CRC Press, Boca Raton, FL.

REYNOLDS, R. T., AND B. D. LINKHART. 1990. Extrapair copulation and extra-range movements in Flammulated Owls. Ornis Scand. 21:74–77.

REYNOLDS, R. T., S. M. JOY, AND D. G. LESLIE. 1994. Nest productivity, fidelity, and spacing of Northern Goshawks in northern Arizona. Stud. Avian Biol. 16:106–113.

REYNOLDS, R. T., AND E. C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. Auk 101:761–779.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83: 423–436.

WARKENTIN, I. G., A. D. CURZON, R. E. CARTER, J. H. WETTON, P. C. JAMES, L. W. OLIPHANT, AND D. T. PARKIN. 1994. No evidence for extrapair fertili-

zations in the Merlin revealed by DNA finger-
printing. Molec. Ecol. 3:229–234.

WESTNEAT, D. F., P. C. FREDERICK, AND R. H. WILEY.
1987. The use of genetic markers to estimate the
frequency of successful alternative reproductive
tactics. Behav. Ecol. Sociobiol. 21:35–45.

WESTNEAT, D. F., AND P. W. SHERMAN. 1997. Density
and extra-pair fertilizations in birds: a comparative
analysis. Behav. Ecol. Sociobiol. 41:205–215.

WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON.
1990. The ecology and evolution of extra-pair
copulations in birds. Current Ornithol. 7:331–369.

FEEDING ASSOCIATIONS BETWEEN WHITE-FRONTED TERNS AND HECTOR'S DOLPHINS IN NEW ZEALAND[1]

STEFAN BRÄGER
*Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand,
e-mail: stefan.brager@stonebow.otago.ac.nz*

Abstract. I investigated the relationship between
White-fronted Terns (*Sterna striata*) associating with
Hector's dolphins (*Cephalorhynchus hectori*) while
feeding in the near-shore environment of New Zealand.
Associations were observed only in the austral spring
and early summer. At this time up to 15.7% of all
dolphin groups were accompanied by terns. The birds
usually joined surface-feeding dolphins with single
terns apparently hovering over single dolphins. Asso-
ciated tern numbers were positively correlated with
dolphin group size and increased significantly with the
duration of the association. Terns were more often as-
sociated with significantly larger dolphin groups and
under calmer sea conditions. Water clarity, however,
appeared to have little influence in the birds' decision
whether or not to associate with a group of foraging
dolphins. The occurrence of feeding associations ap-
peared to be restricted by the occurrence of small, in-
shore moving fish species. The associations are likely
to constitute facultative commensalism by the birds
and may be particularly advantageous during breeding
when energetic demands are high.

*Key words: Cephalorhynchus hectori, feeding as-
sociation, Hector's dolphin, seabird-cetacean inter-
action, Sterna striata, White-fronted Tern.*

Hector's dolphin (*Cephalorhynchus hectori*) is a small,
coastal species endemic to New Zealand. It has been
observed to feed in association with Spotted Shags
(*Stictocarbo punctatus*) and Black-backed Gulls (*Lar-
us dominicanus*) behind fishing trawlers at Banks Pen-
insula, Canterbury (Hawke 1994). Slooten and Daw-
son (1988) mention that feeding associations with
White-fronted Terns (*Sterna striata*) were frequently

observed, but give no further details regarding fre-
quency and intensity of these associations.

I studied the feeding associations of White-fronted
Terns with Hector's dolphins around the South Island
of New Zealand between 1993 and 1997. White-front-
ed Terns as well as Hector's dolphins are known to
feed in neritic waters throughout the year (Bull et al.
1985, Slooten and Dawson 1988). Here I describe the
seasonal pattern of occurrence of feeding associations
and the behavior involved, and investigate the impact
of dolphin group size and environmental factors on
feeding associations.

METHODS

Between 6 November 1993 and 5 April 1997, I spent
a total of 431 days on coastal waters around the South
Island of New Zealand (off Kaikoura, Moeraki, West-
port, Greymouth, Jackson Bay, around Banks Penin-
sula, and in Porpoise Bay; 41–47°S, 167–174°E) study-
ing the behavioral ecology and population biology of
Hector's dolphins. The fieldwork covered all seasons
of the year with 79 field days (18%) in spring (Sep-
tember to November), 197 (46%) in summer (Decem-
ber to February), 84 (19%) in autumn (March to May),
and 71 (17%) in winter (June to August).

Dolphins were observed from a 4.5-m research ves-
sel. Two to eleven hours were spent on the water daily
depending upon weather conditions (surveys were ter-
minated at sea states of 4–5 Beaufort representing
wind speeds of 8–10 m sec^{-1}). Within a day, up to 60
km of coastline were systematically surveyed for the
presence of dolphin groups. Once a group of Hector's
dolphins was encountered, group size, number, and
species of associated seabirds were recorded. Water
depth, sea surface temperature, and water clarity (as
vertical underwater visibility of a 30 cm Secchi disk)
were measured. I attempted to stay with the dolphins
for as long as possible (up to 95 min) and recorded
feeding behaviors. An association was considered a