

- the principle of energy minimization. *Journal of Animal Ecology* 57:411–432.
- MEYER, R. L., AND T. G. BALGOOYEN. 1987. A study and implications of habitat separation by sex of wintering American Kestrels (*Falco sparverius*). Pages 107–123 in *Ancestral Kestrel* (D. M. Bird and R. Bowman, Eds.). Raptor Research Foundation and MacDonald Raptor Research Centre of McGill University, Sainte Anne de Bellevue, Quebec.
- MILLS, G. S. 1975. A winter population study of the American Kestrel in central Ohio. *Wilson Bulletin* 87:241–247.
- MILLS, G. S. 1976. American Kestrel sex ratios and habitat separation. *Auk* 93:740–748.
- MORTON, E. S., J. F. LYNCH, K. YOUNG, AND P. MEHLHOP. 1987. Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? *Auk* 104:133–135.
- NATIONAL CLIMATIC DATA CENTER. 1994. Local climatological data.
- NATIONAL CLIMATIC DATA CENTER. 1995. Local climatological data.
- POWER, H. W. 1980. The foraging behavior of Mountain Bluebirds with emphasis on sexual foraging differences. *Ornithological Monographs*, no. 28.
- PRESS, S. J., AND S. WILSON. 1978. Choosing between logistic regression and discriminant analysis. *Journal of the American Statistical Association* 73:699–705.
- ROHRBAUGH, R. W., AND R. H. YAHNER. 1997. Effects of macrohabitat and microhabitat on nest-box use and nesting success of American Kestrels. *Wilson Bulletin* 109:410–423.
- ROOT, T. L. 1988. *Atlas of Wintering North American Birds*. University of Chicago Press, Chicago.
- SAS INSTITUTE. 1988. *SAS/STAT User's Guide*, release 6.03. SAS Institute Inc., Cary, North Carolina.
- SMALLWOOD, J. A. 1987. Sexual segregation by habitat in American Kestrels wintering in south-central Florida: Vegetative structure and responses to differential prey availability. *Condor* 89:842–849.
- SMALLWOOD, J. A. 1988. A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida. *Auk* 105:36–46.

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Female Hematozoan Infection Reduces Hatching Success but not Fledging Success in Pied Flycatchers *Ficedula hypoleuca*

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ABSTRACT.—We report association between female blood parasite prevalence (percentage of infected birds) just after egg laying and reproductive success in two successive breeding seasons, in a breeding population of Pied Flycatcher *Ficedula hypoleuca* in central Spain. Females infected with *Trypanosoma* spp. had a higher probability of deserting their clutches during the incubation period than noninfected females. Females infected with *Haemoproteus balmoralis* hatched proportionally fewer eggs than noninfected females. Female infected with *H. balmoralis* during the incubation period may have a decreased ability to thermoregulate which may affect their incubation capacity. Fledging success, breeding success, fledgling mass, and tarsus length were not associated with infection of the mother by blood par-

asites during the incubation period, suggesting that females and their mates may compensate during the nestling period for the negative effect of blood parasites during the incubation period.

Most parasites exert an intense selective pressure on their hosts by reducing their condition, survival prospects, mating, or reproductive performances (Loye and Zuk 1991, Møller 1997). That detrimental effect may vary in relation to parasite virulence. In order to understand evolutionary interactions occurring between parasites and their hosts, it is necessary to know the extent to which parasites have a detrimental effect on their hosts' reproduction and survival in wild populations. Reproductive success has been the target of many field studies of birds, because it is expected to relate closely to fitness (Stearns 1992). Blood parasites have been shown to negatively affect reproductive success of their hosts

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because they compete with the host for resources (e.g. review in Møller 1997). If blood parasites have a detrimental effect on their hosts, heavy parasite infections will correlate with low host reproductive success.

Most studies in wild populations have shown a negative effect of parasites on some measure of host reproduction (e.g. clutch size, fledging success; reviewed by Møller et al. 1990, Møller 1997). In particular, many studies have focussed on nestling survival. A problem of those correlative studies is that most birds were sampled at the end of the nestling period, after the main reproductive investment was performed by parents. In birds, high reproductive effort is positively correlated with blood parasite load both for natural clutch sizes (Korpimäki et al. 1993, Allander and Bennett 1995, Dufva 1996, Oppliger et al. 1997, Ilmonen et al. 1999) and for experimentally manipulated clutch sizes (Norris et al. 1994, Richner et al. 1995, Ots and Hórák 1996, Allander 1997, Siikamäki et al. 1997, Wiehn and Korpimäki 1998, Fargallo and Merino 1999, Wiehn et al. 1999; but see Merino et al. 1996). If host reproductive effort increases susceptibility to blood parasite infection or the likelihood that latent, chronic infections may relapse, parasitism may be a consequence of reproductive effort, not its cause (Oppliger et al. 1997). Therefore, studies looking for effects of blood parasites on reproductive success in free living individuals should sample birds before their main reproductive investment is performed. Moreover, because reproduction and immunity are likely to compete for resources (Gustafsson et al. 1994, Sheldon and Verhulst 1996, Lochmiller and Deerenberg 2000, Norris and Evans 2000) and the total amount of energy a bird is able to put into both may depend on food availability (Appleby et al. 1999), studies looking for effects of blood parasites on reproductive success should sample birds under different ecological conditions.

We examined association between blood parasites (*Haemoproteus balmorali*, *Trypanosoma* spp.) and reproductive success of female Pied Flycatchers (*Ficedula hypoleuca*) breeding in central Spain. Blood parasites of females were sampled just after egg laying in two successive breeding seasons. We tested the hypothesis that blood parasites may negatively affect reproductive success of females by examining observed relationship between maternal blood parasite infection and hatching, fledging, and breeding success of Pied Flycatchers.

Methods.—The Pied Flycatcher is a small (12–13 g), migratory, sexually dichromatic, and hole-nesting passerine of European woodlands (Lundberg and Alatalo 1992). Egg laying in our study population typically begins in late May, and clutch size ranges from 2 to 8 eggs with a mode of 6 (Sanz 1997). The female incubates alone and during that period receives part of her food from her mate. Both sexes feed

the young, which fledge within 15–18 days of hatching (Lundberg and Alatalo 1992).

The study was conducted during the springs of 1998 and 1999 in a deciduous forest of Pyrenean oak (*Quercus pyrenaica*) at 1,200 m above sea level in the vicinity of La Granja, central Spain (40°54'N, 04°01'W). Frequent checks of nest-boxes provided data on dates of clutch initiation and clutch size for all breeding pairs. On the day after clutch completion, females were captured and banded with numbered rings. Length of incubation was defined as number of days between completion of clutch and first signs of hatching. Nestlings were measured and ringed on day 13 after hatching (hatching date = day 0). Nestlings were weighed to the nearest 0.1 g and their tarsus length was measured to the nearest 0.01 mm with a digital caliper (Svensson 1992). Unmanipulated broods were visited daily from day 16 onwards to establish numbers of fledged and dead young. Hatching success (proportion of eggs hatched), fledging success (proportion of hatchlings that resulted in fledged young), breeding success (proportion of eggs that resulted in fledged young), and offspring size (fledgling mass and tarsus length) were considered as partial measures of reproductive success.

Blood sampling.—We chose 47 females among 123 Pied Flycatcher pairs trapped in 1998 and 57 females among 142 Pied Flycatcher pairs trapped in 1999. A drop of blood from the left brachial vein was collected in a microcapillary tube and transferred to a glass slide, smeared, air-dried, and fixed in absolute ethanol some hours later. Smears were Giemsa-stained for 45 min to assess hematozoan infections (Merino and Potti 1995, Merino et al. 1997). Parasite analysis was performed by E. Arriero. Smears were microscopically scanned at 200× in search of large parasites such as *Trypanosoma* spp. To prevent the possibility that the symmetry of the blood smear might cause a nonrandom distribution of parasites (Godfray et al. 1987), one-half of each smear was entirely scanned (~300 fields scanned, one-half being chosen at random; Merino and Potti 1995). Subsequently, intraerythrocytic parasites such as *Haemoproteus balmorali* were detected with oil immersion at 1,000× in the other half of the smear. Blood-parasite prevalence was defined as proportion of infected females in the sample.

Statistical procedures.—For females that had been sampled in both years, we randomly picked one observation to be included in the analyses to avoid pseudoreplication. Thus, all birds were entered in the analysis only once. Breeding attempts were classified in two categories, *deserted* (1) and *nondeserted* (0), during the incubation period. Logistic regression analysis was used to explore variables that may influence the female's decision to desert the clutch, that is, year, blood parasite prevalence. Effect of blood parasites on reproductive performance was analysed

TABLE 1. Results of logistic regression analysis of factors determining clutch categories (deserted vs. non-deserted) of female Pied Flycatchers during incubation period.

Variable ($n = 104$)	Estimate	-2logLR	df	P
Study year	0.7590	5.674	1	0.0172
Female parasite status by <i>Trypanosoma</i>	1.2183	25.219	1	<0.001
Female parasite status by <i>Haemoproteus</i>	0.2440	0.914	1	0.3389
Interaction (year \times <i>Trypanosoma</i>)	-0.5020	2.620	1	0.1055
Interaction (year \times <i>Haemoproteus</i>)	-0.5143	4.139	1	0.0419

using ANOVA and entering respective breeding parameters as dependent variables. All statistical analyses were performed using SPSS for Windows® (Norusis 1993) and were two-tailed.

Results.—In the present population, 35 and 16% of females sampled during incubation period were infected with *Haemoproteus balmorali* and *Trypanosoma* spp., respectively ($n = 167$; Sanz et al. 2001).

To study effect of blood parasites on decision of females to desert their clutches, a logistic regression analysis was performed of clutch categories (deserted vs. nondeserted) against *Haemoproteus balmorali* infection status (infected vs uninfected) of females, *Trypanosoma* spp. infection status of females, and

study year. Probability of clutch desertion was dependent on study year (Table 1), but was independent of female *H. balmorali* infection status (Table 1). A higher number of clutches were deserted during the incubation period in 1999 than in 1998 (Fig. 1a). Probability of clutch desertion was significantly dependent on female *Trypanosoma* spp. parasite status (Table 1). More clutches were deserted when females were infected by *Trypanosoma* spp. than when females were uninfected (Fig. 1a). Interaction term between female *Trypanosoma* spp. parasite status and study year was nonsignificant (Table 1), showing that differences in probability of clutch desertion between study years for infected and uninfected females by *Trypanosoma* spp. were in the same direction (Fig. 1a).

There were no significant differences in laying date and clutch size between *Haemoproteus balmorali* infected and uninfected females (Table 2), and between females with or without *Trypanosoma* spp. infection when the effect of study year was controlled (Table 2). *Haemoproteus balmorali* infected females had lower hatching success than uninfected females (Table 2; Fig. 1b), and there were no differences in hatching success between females with or without *Trypanosoma* spp. infection when controlling for the effect of study year (Table 2). There were no differences in incubation period, fledging success, breeding success, fledgling body mass, and tarsus length (mean values per brood) between *H. balmorali* infected and uninfected females (Table 2), and between females with or without *Trypanosoma* spp. infection when the effect of study year was controlled (Table 2).

Discussion.—We have shown that female Pied Flycatchers infected with *Trypanosoma* spp. had a higher probability of clutch desertion during incubation period than uninfected females. Moreover, females infected with *Haemoproteus balmorali* had a lower hatching success than uninfected females. In that southern breeding population, *H. balmorali* was the most common blood parasite for females during incubation period. Species of *H. balmorali* are the most common hemosporidians encountered in free-living birds and are believed to be the least pathogenic of blood parasites (Atkinson and van Riper 1991). However, negative effects may not be easy to document, especially

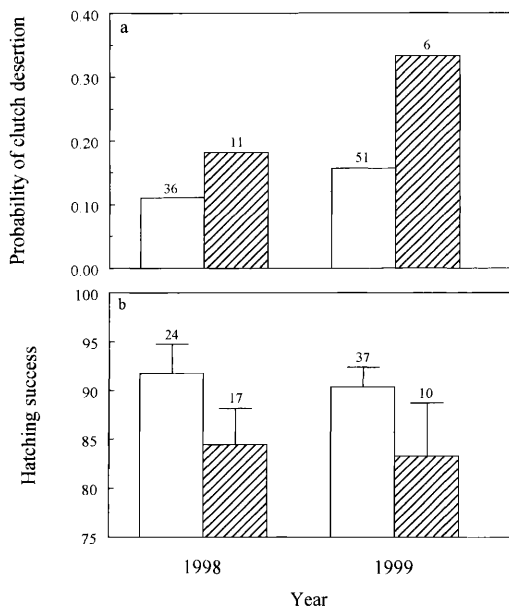


FIG. 1. (A) Probability of clutch desertion according to study year and female infection by *Trypanosoma* spp. (open bars = uninfected females; hatched bars = infected females) during incubation period. (B) Mean hatching success according to study year and female infection by *Haemoproteus balmorali* (open bars = uninfected females; hatched bars = infected females). The error bars represent the standard error of the mean. Numbers above bars are sample sizes.

TABLE 2. Analyses of variance of reproductive parameters of female Pied Flycatchers in relation to blood parasites prevalences (*Haemoproteus balmorali*, *Trypanosoma* spp.) and study years.

	n	<i>Haemoproteus</i>		<i>Trypanosoma</i> spp.		Study year	
		F	P	F	P	F	P
Laying date	104	2.36	0.13	0.03	0.87	11.20	<0.001
Clutch size	104	2.42	0.12	0.08	0.78	16.39	<0.001
Incubation period (days)	88	0.45	0.50	1.11	0.29	8.84	0.004
Hatching success (%)	88	5.18	0.025	0.01	0.92	0.63	0.43
Fledging success (%)	88	3.34	0.07	1.26	0.26	2.69	0.10
Breeding success (%)	88	0.00	0.94	0.43	0.51	2.05	0.16
Fledgling mass (g)	84	1.91	0.17	0.38	0.54	1.19	0.28
Fledgling tarsus (mm)	84	0.47	0.49	0.34	0.56	5.00	0.028

in wild birds, without manipulating parasite load (Bennett et al. 1993).

Most studies in free-living breeding birds have focussed on nestling period to study association between blood parasites and host reproductive success (review in Møller et al. 1990, Møller 1997). That may be due to the general perception that incubation period is a time of reduced energy demand compared to other phases of the reproductive period. However, in altricial species, there is no convincing evidence of differences in female energy expenditure during incubation as compared to energy expenditure during the nestling period (Williams 1995, Thomson et al. 1998). In this study, we presented evidence that desertions during the incubation period were higher and hatching success lower for infected females than uninfected females.

Evidence of effects of different genera of blood parasites on breeding performance during incubation period has been reported in two passerine species. Dufva (1996) has shown that female Great Tits (*Parus major*) carrying *Trypanosoma* hatched proportionally fewer eggs compared to females without *Trypanosoma*. However, female Great Tits were sampled when nestlings reached an age of 13 days, and a relatively small number of birds were infected by that blood parasite (three females in four years; Dufva 1996). Sample size is too small to support the conclusion that lower hatching success was a consequence of parasitism (Dufva 1996). In another study, Widemo (1989) has reported that Collared Flycatchers (*Ficedula albicollis*) suffering from malaria take longer to incubate their eggs (see reference in Møller et al. 1990). On the other hand, physiological studies of hemotozoan infections have shown that acute infections may have significant effects on oxygen transport and ability to thermoregulate in birds (Hayworth et al. 1987). Hayworth et al. (1987) found that captive canaries infected by *Plasmodium relictum* have decreased ability to thermoregulate and lowered oxygen capacity at the crisis stage when peripheral parasitemia reaches a peak. That study suggested that hemotozoan infections may be especially important if the peak of parasitemia coincides with

thermally stressing conditions (Hayworth et al. 1987). Females infected by blood parasites during incubation period may have decreased ability to thermoregulate which might affect their incubation capacity. Moreover, there may be a trade-off during the incubation period between resources that females invest in reproductive activities and those invested in mounting an immune response to blood parasites (Gustafsson et al. 1994, Sheldon and Verhulst 1996, Lochmiller and Deerenberg 2000, Norris and Evans 2000).

Our observational study shows that females infected with *Haemoproteus balmorali* experience a lower hatching success, and that those females or their mates may compensate for that negative effect during the nestling period. *Haemoproteus balmorali* infected females tended to have higher fledging success than noninfected ones, but that difference was not statistically significant. That may explain why there were no differences in breeding success, fledgling mass, and tarsus length between *H. balmorali* infected and uninfected females. Thus, *H. balmorali* infected female Pied Flycatchers might not suffer from reduced individual fitness after egg laying. We suggest that blood parasitemia might have important consequences on maternal reproductive performance during incubation period, a thermally stressful period. Females' blood-parasite loads were measured at the beginning of the incubation period and an association with their reproductive success was shown. We found negative effects of blood parasites only during the incubation period: higher probability of clutch desertion or lower hatching success.

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LITERATURE CITED

- ALLANDER, K. 1997. Reproductive investment and parasite susceptibility in the Great Tit. *Functional Ecology* 11:358–364.
- ALLANDER, K., AND G. F. BENNETT. 1995. Retardation of breeding onset of Great Tits (*Parus major*) by blood parasites. *Functional Ecology* 9:677–682.
- APPLEBY, B. M., M. A. ANWAR, AND S. J. PETTY. 1999. Short-term and long-term effects of food supply on parasite burdens in Tawny Owls, *Strix aluco*. *Functional Ecology* 13:315–321.
- ATKINSON, C. T., AND C. VAN RIPER III. 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium*, *Leucozytozoon* and *Haemoproteus*. Pages 19–48 in *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (J. E. Loye and M. Zuk, Eds.). Oxford University Press, Oxford.
- BENNETT, G. F., M. A. PEIRCE, AND R. W. ASHFORD. 1993. Avian haematozoa: Mortality and pathogenicity. *Journal of Natural History* 27:993–1001.
- DUFVA, R. 1996. Blood parasites, health, reproductive success, and egg volume in female Great Tits *Parus major*. *Journal of Avian Biology* 27:83–87.
- FARGALLO, J. A., AND S. MERINO. 1999. Brood size manipulation modifies the intensity of infection by haematozoa in female Blue Tits *Parus caeruleus*. *Ardea* 87:261–268.
- FORBES, M. R. L. 1993. Parasitism and host reproductive effort. *Oikos* 67:444–450.
- GODFRAY, R. D., A. M. FEDYNICH, AND D. B. PENCE. 1987. Quantification of hematozoa in blood smears. *Journal of Wildlife Disease* 23:558–565.
- GUSTAFSSON, L., D. NORDLING, M. S. ANDERSSON, B. C. SHELDON, AND A. QVARNSTROM. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London, Series B* 346:323–331.
- HAYWORTH, A. M., C. VAN RIPER III, AND W. W. WEATHERS. 1987. Effects of *Plasmodium relictum* on the metabolic rate and body temperature in canaries (*Serinus canarius*). *Journal of Parasitology* 73:850–853.
- ILMONEN, P., H. HAKKARAINEN, V. KOIVUNEN, E. KORPIMÄKI, A. MULLIE, AND D. SHUTLER. 1999. Parental effort and blood parasitism in Tengmalm's Owl: Effects of natural and experimental variation in food abundance. *Oikos* 86:79–86.
- KORPIMÄKI, E., H. HAKKARAINEN, AND G. F. BENNETT. 1993. Blood parasites and reproductive success of Tengmalm's Owls: Determental effects on females but not on males? *Functional Ecology* 7:420–436.
- LOCHMILLER, R. L., AND C. DEERENBERG. 2000. Trade-offs in evolutionary immunology: Just what is the cost of immunity? *Oikos* 88:87–98.
- LOYE, J. E., AND M. ZUK, EDs. 1991. *Bird-Parasite Interactions: Ecology, Evolution and Behaviour*. Oxford University Press, Oxford.
- LUNDBERG, A., AND R. V. ALATALO. 1992. *The Pied Flycatcher*. Poyser, London.
- MERINO, S., AND J. POTTI. 1995. High prevalence of hematozoa in nestlings of a passerine species, the Pied Flycatcher (*Ficedula hypoleuca*). *Auk* 112: 1041–1043.
- MERINO, S., J. POTTI, AND F. A. FARGALLO. 1997. Blood parasites of passerine birds from central Spain. *Journal of Wildlife Disease* 33:638–641.
- MERINO, S., J. POTTI, AND J. MORENO. 1996. Maternal effort mediates the prevalence of trypanosomes in the offspring of a passerine bird. *Proceedings of the National Academy of Science USA* 93: 5726–5730.
- MØLLER, A. P. 1997. Parasites and the evolution of host life history. Pages 105–127 in *Host-Parasite Evolution: General Principles and Avian Models* (D. Clayton and J. Moore, Eds.). Oxford University Press, Oxford.
- MØLLER, A. P., K. ALLANDER, AND R. DUFVA. 1990. Fitness effects of parasites on passerine birds: A review. Pages 269–280 in *Population Biology of Passerine Birds: An Intergrated Approach* (J. Blondel, A. Gosler, J.-D. Lebreton, and R. H. McCleery, Eds.). Springer-Verlag, Berlin.
- NORRIS, K., M. ANWAR, AND A. F. READ. 1994. Reproductive effort influences the prevalence of haematozoan parasites in Great Tits. *Journal of Animal Ecology* 63:601–610.
- NORRIS, K., AND M. R. EVANS. 2000. Ecological immunology: Life history trade-offs and immune defense in birds. *Behavioral Ecology* 11:19–26.
- NORRIS, M. J. 1993. *SPSS Advanced Statistics User's Guide*. SPSS, Chicago.
- OPPLIGER, A., P. CHRISTE, AND H. RICHNER. 1997. Clutch size and malarial parasites in female Great Tits. *Behavioral Ecology* 8:148–152.
- OTS, I., AND P. HÖRAK. 1996. Great Tits *Parus major* trade health for reproduction. *Proceedings of the Royal Society of London, Series B* 263:1443–1447.
- RICHNER, H., P. CHRISTE, AND A. OPPLIGER. 1995. Parental investment affects prevalence of malaria. *Proceedings of the National Academy of Science USA* 92:1192–1194.
- SANZ, J. J. 1997. Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca*. *Ibis* 139:107–114.
- SANZ, J. J., E. ARRIERO, J. MORENO, AND S. MERINO. 2001. Interactions between hemoparasite status

- and female age in the primary reproductive output of Pied Flycatchers. *Oecologia* 126:339–344.
- SHELDON, B. C., AND S. VERHULST. 1996. Ecological immunology: Costly parasite defenses and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* 11:317–321.
- SIKKAMÄKI, P., O. RÄTTI, M. HOVI, AND G. F. BENNETT. 1997. Association between haematozoan infections and reproduction in the Pied Flycatcher. *Functional Ecology* 11:176–183.
- STEARNS, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- SVENSSON, L. 1992. *Identification Guide to European Passerines*. Fingraf AB, Stockholm, Sweden.
- THOMSON, D. L., P. MONAGHAN, AND R. W. FURNESS. 1998. The demands of incubation and avian clutch size. *Biological Review* 73:293–304.
- WIDEMO, F. 1989. Effect of blood parasites on the Col-lared Flycatcher *Ficedula albicollis*. Honors thesis, Department of Zoology, Uppsala University, Uppsala, Sweden.
- WIEHN, J., AND E. KORPIMÄKI. 1998. Resource levels, reproduction and resistance to haematozoan infections. *Proceedings of the Royal Society of London, Series B* 265:1197–1201.
- WIEHN, J., E. KORPIMÄKI, AND I. PEN. 1999. Haematozoan infections in the Eurasian Kestrel: Effects of fluctuating food supply and experimental manipulation of parental effort. *Oikos* 84:87–98.
- WILLIAMS, J. B. 1997. Energetics of avian incubation. Pages 375–415 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.

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Diving Depths of Shearwaters

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ABSTRACT.—Maximum diving depths were measured for shearwaters breeding on Cousin Island, Seychelles. Eighty-three percent of 23 Wedge-tailed Shearwaters (*Puffinus pacificus*) dived, and their mean maximum depth was 14 m (SD = 23 m, range 1–66 m, $N = 19$). All Audubon's Shearwaters (*P. lherminieri*) dived, and their mean maximum depth was 15 m (SD = 12 m, range 6–35 m, $N = 7$). These data contradict the hypothesis that tropical shearwaters should not specialize in underwater foraging. They are capable of exploiting deep prey unavailable to most other tropical seabirds. Five *Puffinus* species (temperate and tropical) attained allometrically scaled maximum depths comparable to those of penguins and alcid.

It has long been known that shearwaters dive beneath the ocean to forage, using their feet and wings for propulsion (Brown et al. 1978, 1981), and show anatomical adaptations for this mode of foraging (Kuroda 1954, Warham 1990). Simple depth gauges measuring the maximum depths indicate some remarkably deep dives attained by shearwaters (Wei-

merskirch and Sagar 1996, Weimerskirch and Chérel 1998, Keitt et al. 2000). More sophisticated time-depth-recorders (TDRs), which indicate time spent at various depths and trace individual dives, have revealed much of the underwater foraging behavior of penguins, alcid, and cormorants (Kooyman 1989, Croll et al. 1992, Wilson 1995, Watanuki et al. 1996), but have not been applied to shearwaters. I report maximum depths attained by two tropical shearwaters, Wedge-tailed (*Puffinus pacificus*) and Audubon's (*P. lherminieri*) shearwaters, breeding on Cousin Island, Seychelles (4°20'S; 55°40'E), and review data on diving depths of other shearwaters. I examine the hypothesis that tropical shearwaters should not specialize in underwater foraging (Brown et al. 1978), and discuss the role of diving in tropical shearwaters.

Methods.—Maximum-depth gauges were made from flexible plastic tubing with internal diameter 0.8 mm, lined with a thin layer of icing sugar and sealed at one end. Gauges were 70–120 mm long on Wedge-tailed Shearwaters, and 70–90 mm long on Audubon's Shearwaters. As the gauge is submerged, the increasing pressure forces water into the tube, dissolving the sugar and leaving a record of the deepest dive (Kooyman et al. 1971, Burger and Wilson 1988, Hedd et al. 1997). The equation provided

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