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LEG ABNORMALITIES AND LEUCOCYTE PROFILES IN THE EUROPEAN STORM-PETREL (*HYDROBATES P. PELAGICUS*) FROM THE FAROE ISLANDS

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ABSTRACT.—Although abnormal or injured legs are not uncommon in *Hydrobatidae*, they are rarely investigated. We aimed in this study to estimate the frequency of leg abnormalities and determine health status (expressed by leucocyte profile) in molecularly sexed European Storm-Petrels (*Hydrobates p. pelagicus*) captured on the Faroe Islands. We found that 2.4% of individuals captured during the breding season had some leg abnormalities. Half of the birds with abnormalities had puffinosis-like changes, while the rest were missing some part of the leg. Both types of abnormalities were recorded in the two sexes with similar frequency. The proportion of the birds with leg abnormalities seems to be relatively low compared to other *Procellariiformes*, and stable over time. Despite the apparent disability of the birds with leg abnormalities, we found no significant effect of abnormality status on the leucocyte profile. *Received 28 January 2014. Accepted 24 May 2014.*

Key words: health status, hemathological parameters, *Hydrobatidae*, puffinosis, storm-petrel.

Although abnormal or injured legs are not uncommon in *Hydrobatidae*, they have been rarely investigated. There are several studies reporting leg damage in these birds, but only a few of them were conducted in a systematic way (e.g., Love 1984, Kirkham et al. 1987). Of these studies, it was not always clear what the authors considered a leg abnormality. Moreover, existing reports suggest that there is great variation in the extent of occurrence of leg abnormalities among species and populations (e.g., 0.6–12.8% in the Leach's Storm-Petrel *Oceanodroma leucorhoa* [Morse and Buchhersteir 1977, Kirkham et al. 1987 and references therein], 3.5–7.0%, in the Band-rumped Storm-Petrel *Oceanodroma castro* [Allan 1962, Harris 1969], 0.7–7.5% in the European Storm-Petrel *Hydrobates p. pelagicus* [Lovegrove 1968, Love 1984, Bowey 1995, Minguez 1996]).

The causes of the leg damage in *Hydrobatidae* remain poorly understood. Some authors have suggested that it may be a consequence of attacks of subsurface predators on the birds while they are foraging or resting on the water's surface (Harrison 1955; Threlfall 1969, 1974; Kirkham et al. 1987). Seabirds staying at sea overnight are more likely to have leg injuries than those spending the night in the colony (Zavalaga et al. 2012). An epizootic disease may be another cause of leg damage, as some birds have been reported to have blisters/lesions on the foot webs and swollen joints, typical symptoms of puffinosis (Waters 1964, Jensen 1999). The disease is probably caused by an arthropod-borne virus (Nuttall et al. 1982, Brooke 1990) and has been reported in other *Procellariiformes* such as the Manx Shearwater *Puffinus puffinus* (Dane 1948; Miles and Stoker 1948, 1953; Harris 1965; Kirkwood et al. 1995) and the Northern Fulmar *Fulmarus glacialis* (MacDonald et al. 1967). There were also suggestions that gulls *Larus* spp. or puffins *Fratercula* spp. attacked and caused leg injuries to petrels (Threlfall 1974), or the injuries are related to digging nest burrows (Kirkham et al. 1987), but these hypotheses seem to be the least supported.

Additionally, the effects of leg damage on a petrel's health status and/or survival are largely unknown. There are incidental records of retrapping European Storm-Petrels with leg abnormalities after a year, suggesting their apparent survival (Scott 1970). There is also some evidence that leg damage did not appreciably impair the breeding success in the Band-rumped Storm-Petrel (Allan 1962, Harris 1969). More systematic studies did not reveal significant differences in body mass between birds with and without leg abnormalities (Lovegrove 1968, Love 1984). However, the number of birds compared was low, and only body mass was considered, which as a single index may not be the best condition

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estimate (e.g., Ewenson et al. 2001, Jakubas et al. 2008).

Investigating the frequency and nature of leg damages in petrel populations as well as examining their health status in a systematic way should help to understand both the causes and effects of the leg abnormalities. Depending on the causes and effects of the abnormalities, such a study may be a way of monitoring the health status of the birds' populations. We aimed in this study to estimate the frequency of the leg abnormalities, provide an estimate of health status using leucocyte profiles, for the European Storm-Petrel on the Faroe Islands. The species is the smallest among *Procellariiformes*. Thus, if the leg abnormalities are associated with some physical and/or physiological (immunological) constraints, the fitness consequences may be relatively higher compared to other *Procellariiformes*. The Faroe Islands are believed to host the largest breeding colonies of European Storm-Petrels in the world (BirdLife 2004). Approximately 40 years ago, 2.3% of the European Storm-Petrels on the Faroe Islands had leg damage (Lovegrove 1968).

MATERIALS AND METHODS

We carried out the study in a large breeding colony of European Storm-Petrels on Nólsoy Island (61° 59′ N, 06° 47′ W) on the Faroe Islands. We captured the birds in a mist-net during the incubation period (6–21 Aug) in 2013. We marked all birds using a metal ring with an individual number (Natural History Museum of Denmark) and examined their feet/legs. In total, we considered 879 birds. Recorded leg abnormalities varied considerably among the individuals, both in term of a character and extent of the changes. However, two distinct groups of abnormalities could be distinguished: 1) puffinosis-like changes (swollen joints, changed pigmentation; Fig. 1a–c) and 2) lack of some bones or part of the bones in the leg (Fig. 1d–e). We sampled blood from all birds that had leg abnormalities ($n = 21$), and from 44 randomly chosen birds without leg abnormalities (all with an apparent brood patch indicating breeding; hereafter called a control group [Fig. 1f]). We aged all birds that we captured according to criteria by Bolton and Thomas (2001), and all individuals considered in the present study were adults.

We took a small blood sample (10 μL) by pricking the underwing vein with a sterile, disposable needle (Owen 2011). For the purpose of the immunological analyses, we made a blood smear from half of the amount of blood taken. We air-dried the smears in the field and stained them in the laboratory using the May-Grünewald-Giemsa method (Lille 1977) ~3 weeks later. The rest of the blood was preserved in 96% pure ethanol for further molecular sexing. We released the birds unharmed after ~5 min of handling.

To estimate the birds' health status, we established a leucocyte profile, which included a) relative abundance of each white blood cell type, b) total number of leucocytes and the number of the most common types of the white blood cells (heterophils, lymphocytes) per 10,000 erythrocytes, and c) a heterophils to lymphocytes ratio. The leucocyte profiles provide a convenient measure of integrated immune function (Davis 2005, Salvante 2006). Elevated total number of leucocytes indicates an inflammatory process in response to both microbiological and macroparasite infections (e.g., Dein 1986). Lymphocytes are responsible for pathogen-specific immune response (Fudge 1989; but see Dufva and Allander 1995) and their increased numbers can be found during parasitic infection (Ots and Hõrak 1998) as well as any immunological challenges (Eeva et al. 2005). Heterophils are non-specific phagocytozing cells that enter the tissues during an inflammation, particularly because of a microbial challenge (Rose et al. 1979, Hawkey et al. 1985, Campbell 1995, Maxwell and Robertson 1998). They increase in number during stress, trauma, and chronic bacterial infections. The heterophils to lymphocytes ratio (H/L) is often used as stress indicator in birds (reviewed in Davis et al. 2008). This ratio is known to increase during infectious diseases and/or starvation. The remaining 20% of the leucocytes are represented by eosinophils, which are associated with the inflammation process and defense against parasites (Maxwell 1987), monocytes, which are phagocytic cells playing a role in defense against infections and bacteria (Campbell 1995) and basophils, the function of which is not fully understood but is thought to involve inflammation (Campbell 1995).

To determine the leucocyte profile, we examined one cell-layer, non-overlapping microscope fields of each smear at 1000× magnification under oil immersion. For each smear, we counted 100 leucocyte cells and identified them by type. Additionally, we estimated the total number of leucocytes and calculated abundance of the most

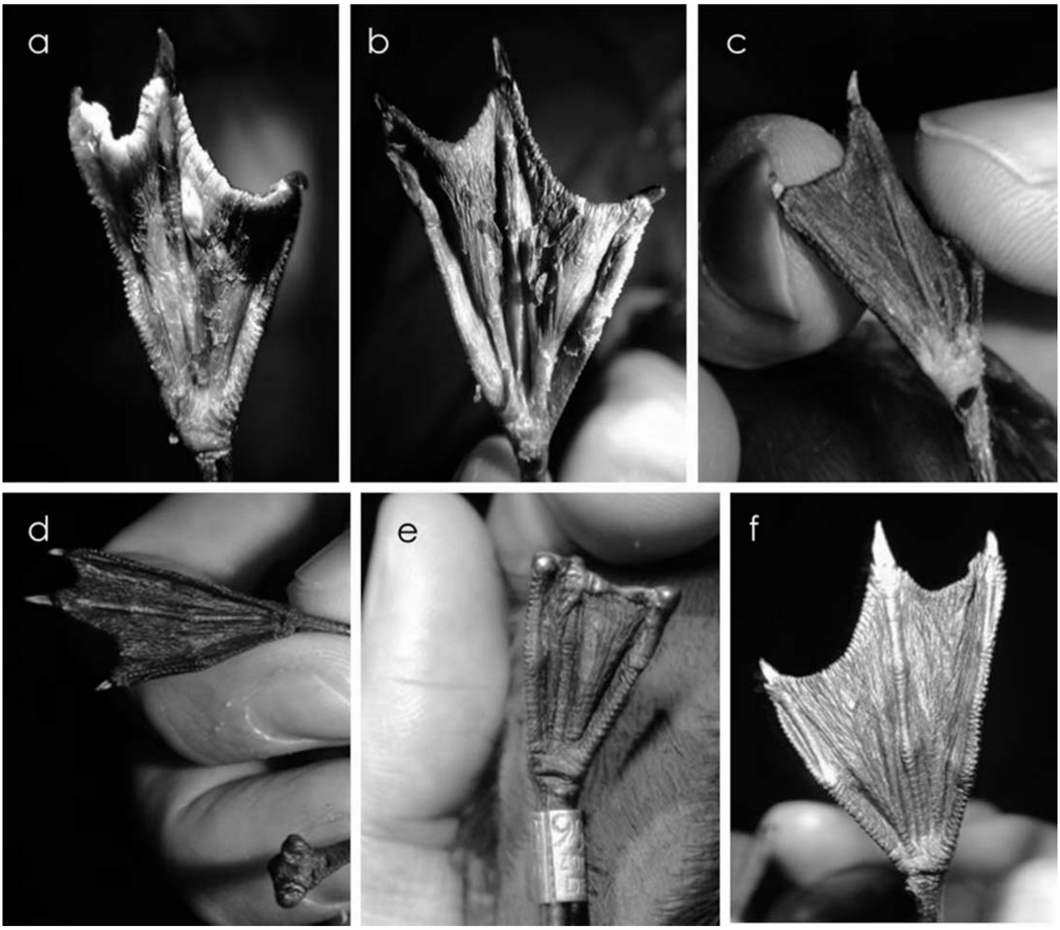

FIG. 1. Legs of European Storm-Petrels captured in the Faroe Islands in 2013 with puffinosis-like changes (swollen joints, changed pigmentation; a–c), with lack of some part of the leg (d–e), and normal (f).

common types of the white blood cells (heterophils, lymphocytes) per 10,000 erythrocytes. We did this by counting red blood cells per field and multiplying the outcome by the number of fields within which leucocytes had to be counted to reach 100 (Ots et al. 1998). All leucocyte counts were performed by the same person (AK), who did not know the status of the examined smears.

We extracted DNA from the blood following evaporation of the alcohol using the Blood Mini kit (A&A Biotechnology, Gdynia, Poland). We performed molecular sexing with the primer pair 2550F and 2718R according to the protocol described by Griffiths et al. (1998), using 50 °C for the annealing temperature in the polymerase chain reaction. The primers amplify introns on the CHD-W and CDH-Z genes located on the W and Z avian sex chromosomes (Fridolfsson and Ellegren 1999). The difference between the two fragments (ca. 200 bp) was clearly visible in UV-light when separating on 2% agarose gel, stained with Midori Green.

Because of very low numbers or absence of basophils, eosinophiles, and monocytes in most of the blood smears, we did not consider these leucocytes in statistical analyses and only examined their abundance per 100 leucocytes. The other leucocyte variables (the proportion of heterophils and lymphocytes, the ratio of these two [H/L], and the number of the heterophils, lymphocytes and total leucocytes per 10,000 erythrocytes) were normalized before further analyses using an arcsin square-root transformation (Zar 1999). However, we used raw data to

TABLE 1. Leucocyte profile of European Storm-Petrels with (two types) and without leg-abnormalities (control group), and results of statistical comparisons of particular variables among the three groups. The values of the variables were expressed by mean ± SD and range.

Variable	Puffinosis-like changes (n = 10)	Lack of part of the leg (n = 11)	Control group (n = 44)	F	P
% of lymphocytes (L)	46.50 ± 6.55 (38–61)	45.82 ± 11.23 (34–65)	49.35 ± 14.81 (25–84)	0.43	0.65
% of heterophils (H)	53.50 ± 6.55 (39–62)	54.18 ± 11.23 (35–66)	50.88 ± 14.67 (16–75)	0.38	0.69
H/L ratio	1.19 ± 0.28 (0.64–1.63)	1.30 ± 0.53 (0.54–1.94)	1.21 ± 0.64 (0.19–3.01)	0.21	0.81
H per 10^4 eryth.	0.87 ± 0.19 (0.60–1.25)	0.97 ± 0.28 (0.64–1.48)	0.97 ± 0.30 (0.33–1.75)	0.38	0.69
L per 10^4 eryth.	0.77 ± 0.22 (0.44–1.25)	0.83 ± 0.34 (0.46–1.71)	1.19 ± 1.25 (0.39–5.95)	0.85	0.43
total leucocytes per 10^4 eryth.	1.64 ± 0.36 (1.15–2.50)	1.81 ± 0.42 (1.23–2.63)	2.16 ± 1.35 (1.02–7.26)	1.00	0.37
% of basophils	0.47 ± 1.11 (0–3)	0.20 ± 0.44 (0–1)	0.47 ± 1.33 (0–7)	-	-
% of eosinophils	0.47 ± 0.85 (0–2)	0.92 ± 1.20 (0–3)	1.38 ± 1.82 (0–7)	-	-
% of monocytes	0.58 ± 0.98 (0–2)	1.35 ± 1.39 (0–4)	1.15 ± 1.33 (0–5)	-	-

present reference values for the leucocyte variables in the examined individuals (Table 1). We performed separate analyses of ANOVA (in GLM mode) for each leucocyte variable (dependent variable) with a leg-group as a fixed factor. Since minor bone loss (lack of distal part of a digit) in the leg may influence the health of a bird less than loss of a major part (e.g., whole *acropodium* or more), we also performed ANOVA analyses excluding the three birds (see results) that had only minor changes. Because of low sample size, the sex of the birds was not included in the model. All analyses were performed in STATISTICA 9.1 (StatSoft Inc., USA).

RESULTS

Of 879 birds examined, 21 (2.4%) were found to have some type of leg abnormality. Ten birds (1.1%) had puffinosis-like changes (Fig. 1a–c) and 11 individuals (1.2%) were recorded as missing some part of the leg (73% were lacking a complete acropodium or more, Fig. 1d; 27% were missing distal parts of one or more digits, Fig. 1e). Puffinosis-like changes occured usually on both legs while lack of some parts was recorded only for a single leg (right or left). Both types of abnornalities were recorded in two sexes at equal frequencies (puffinosis-like changes: six males and four females, lack of some part of the leg: seven males and four females; Fisher's exact tests, both $P > 0.05$).

There were no significant differences between the birds with leg-abnormalities and the control group in any variable of the leucocyte profile studied (ANOVA, all $P > 0.05$; Table 1). Also, after excluding from the analyses the three birds lacking only minor parts of the leg, no significant differences in any of the examined variables were found among the three leg-groups (ANOVA, all $P > 0.05$).

DISCUSSION

The proportion of European Storm-Petrels with leg abnormalities recorded in our study (2.4%) falls somewhere in between the range for petrels in general (0.6–12.8%, see Introduction for references). The value is also very similar to 2.3%, reported for the birds from roughly the same location by Lovegrove (1968) in the 1960s. Thus, the proportion of the birds affected seems to be relatively low and stable over time.

The observed leg abnormalites in European Strom-Petrels may have different origins. Individuals which were missing some part of the leg may have acquired the injuires on the ground, when entering or leaving rocky sites, scraping in the substrate, or bearing attacks by predatory fish, gulls, or puffins (Harrison 1955, Threlfall 1969, 1974, Kirkham et al. 1987). However, the puffinosis-like changes clearly caused an infection or disease. Because of similar proportions of birds with puffinosis-like changes and missing leg parts, it is possible that the latter condition is a consequence of the puffinosis-like changes.

If the main cause of the leg abnormalities is an infectious disease, this may have several implications in the context of the general health status of the studied population. We can speculate that despite apparent presence of the disease in the environment, the birds remain resistant. Only a limited number of birds are affected, and those individuals in which the disease develops seem to survive the infection. This might indicate that the disease persists in the environment for a very long time, during which a sufficient immunological mechanism may have evolved as a defense against the pathogen. Alternatively, European Storm-Petrels could have a very strong general immunological system. In any case, given the lack of significant differences in the leucocyte profiles between the individuals with and without the leg abnormalities, it seems that birds cope well. Obviously, it cannot be entirely ruled out that the birds with leg abnormalities perform without any impairment. First, it is possible that only those individuals with relatively small abnormalities survive, as birds with significant damage to both legs could not fly off the ground. Second, the breeding success of disabled males may be lowered. The mating behavior of European Storm-Petrels is not well known, but assuming it is typical for birds, an injured male mounting a female may have problem with balance and therefore insemination. As a consequence, the female may seek extra-pair copulations. Thus, the pair might raise young successfully (Allan 1962, Harris 1969), but the offspring might not be genetically related to the male of the attending pair.

The lack of differences in the leucocyte profiles betwen the individuals with and without the leg abnormalities is unexpected, given the functions of the various leucocytes and nature of the pathogen. A coronovirus has been suggested as an etiological agent of the puffinosis (Miles and Stoker 1948, 1953; Nuttal et al. 1982). If so, the presence of the virus in individuals with apparent sypmtoms of the disease should be reflected in the leucocyte profiles. As that was not the case, another agent, such as fungus, could be responsible for the disease. In fact, we could smell a specific rancid, cheesy-like scent while handling the birds with the puffinosis-like changes on the legs. As long as the fungus proliferates superficially, it may not cause the immunologuical response (Osawa et al. 1998). In the case of birds that are missing leg parts, similarity to the control group in leucocyte profiles could be explained by the birds' recovery. It is also possible that the control group considered in the present study might have included some infected individuals that enlarged the ranges for the studied variables and so obscured potential differences between the infected and control groups.

Nevertheless, lack of differences in some hemathological variables between the individuals with and without the puffinosis has been reported by Kirkwood et al. (1995) studying fledglings of a larger *Procellariiformes*, the Manx Shearwater. Also, no significant difference in the ratio of heterophils and lymphocytes has been found in Northern Fulmars infected and free of parasitic gastrointestinal helminthes (the H/L ratios : 0.57 and 0.63, respectively; Mallory et al. 2007). On the other hand, the leucocyte profiles have been found to be very useful when examining the health status of birds tagged with a geolocator, in comparison to untagged individuals in another *Procellariiformes* species, the Thin-billed Prion *Pachyptila belcheri*. The study clearly showed that birds with the device had higher H/L ratio (1.71) and proportion of heterophils (57.2%) than the control ones (H/L: 0.97; heterophils: 42.4%) (Quillfeldt et al. 2012).

The present study documented a very low frequency of leg abnormalities in the population of the European Storm-Petrels on the Faroe Islands, and no effect of leg abnormalities on a bird's health status. This is interesting *per se* and makes a valuable contribution to the scant literature concerning the effects of abnormalities in wild birds. Also, presented leucocyte profiles may constitute reference values for the studied species/population during the incubation period, which could be used for a comparison in future studies.

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LITERATURE CITED

Allan, R. G. 1962. The Madeiran Storm-Petrel *Oceanodroma castro*. Ibis 103:274–295.

BirdLife. 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife Conservation Series Number 12, Cambridge, UK.

Bolton, M. and R. Thomas. 2001. Moult and ageing of storm-petrels *Hydrobates pelagicus*. Ringing and Migration 20:193–201.

Bowey, K. 1995. European Storm-Petrels without their toes. British Birds 88:111.

Brooke, M. 1990. Pages 144–167 *in* The Manx Shearwater. T. & A. D. Poyser, London, UK.

Campbell, T. W. 1995. Avian hematology and cytology. Iowa State University Press, Ames, Iowa.

Dane, D. 1948. A disease of Manx Shearwaters *(Puffinus puffinus)*. Journal of Animal Ecology 17:158–164.

Davis, A. K. 2005. Effects of handling time and repeated sampling on avian white blood cell counts. Journal of Field Ornithology 76:334–338.

DAVIS, A. K., D. L. MANEY, AND J. C. MAERZ. 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. Functional Ecology 22:760–772.

DEIN, J. 1986. Hematology. Pages 174–191 *in* Clinical avian medicine (G. J. Harrison, and W. R. Harrison, Editors). Saunders, London, UK.

DUFVA, R. AND K. ALLANDER. 1995. Intraspecific variation in plumage coloration reflects immune response in Great Tit (*Parus major*) males. Functional Ecology 9:785–789.

EEVA, T., D. HASSELQUIST, A. LANGEFORS, L. TUMMELEHT, M. NIKINMAA, AND P. ILMONEN. 2005. Pollution related effects on immune function and stress in a free-living population of Pied Flycatcher *Ficedula hypoleuca*. Journal of Avian Biology 36:405–412.

EWENSON, L., R. A. ZANN, AND G. R. FLANNERY. 2001. Body condition and immune response in wild Zebra Finches: effects of capture, confinement and captive-rearing. Naturwissenschaften 88:391–394.

FRIDOLFSSON, A. K. AND H. ELLEGREN. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

FUDGE, A. M. 1989. Avian hematology: identification and interpretation. Pages 284–292 *in* Proceedings of Association of Avian Veterinary Annual Meeting, Seattle, Washington, USA.

GRIFFITHS, R., M. C. DOUBLE, K. ORR, AND R. J. DOWSON. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

HARRIS, M. P. 1965. Puffinosis among Manx Shearwaters on Skokholm. British Birds 58:426–433.

HARRIS, M. P. 1969. The biology of storm-petrels in the Galapagos Islands. Proceedings of California Academy of Sciences 37:95–165.

HARRISON, I. M. 1955. Fish and other aquatic fauna as predators of birds. Bulletin of the British Ornithologists' Club 75:110–113.

HAWKEY, C., H. J. SAMOUR, G. M. HENDERSON, AND M. G. HART. 1985. Haematological findings in captive Gentoo Penguins (*Pygoscelis papua*) with bumblefoot. Avian Pathology 14:251–256.

JAKUBAS, D., K. WOJCZULANIS-JAKUBAS, AND R. KREFT. 2008. Sex differences in body condition and hematological parameters in the Little Auk *Alle alle* during the incubation period. Ornis Fennica 85:90–97.

JENSEN, J.-K. 1999. European Storm-Petrels losing toes through disease. British Birds 92:481.

KIRKHAM, I. R., W. A. MONTEVECCHI, O. J. LIEN, B. O. SKLEPKOVYCH, AND R. G. BUTLER. 1987. Damage to Leach's Storm-Petrel feet. Ornis Scandinavica 18:61–64.

KIRKWOOD, J. K., A. CUNNINGHAM, C. HAWKEY, J. HOWLETT, AND C. M. PERRINS. 1995. Hematology of Fledgling Manx Shearwaters (*Puffinus puffinus*) with and without 'puffinosis.' Journal of Wildlife Disease 31:96–98.

LILLE, R. D. 1977. Conn's biological stains. Williams & Wilkins Company, Baltimore, Maryland, USA.

LOVE, J. A. 1984. Leg injuries in small petrels. Seabirds 7:71–73.

LOVEGROVE, R. R. 1968. Storm petrels and Leach's Petrels. Pages 11–19 *in* Expedition to the Faroe Islands. Exploration Group, Brathay, UK. Unpublished report.

MACDONALD, J. W., D. A. MCMARTIN, K. C. WALKER, M. CARINS, AND R. H. DENNIS. 1967. Puffinosis in fulmars in Orkney and Shetland. British Birds 60:356–360.

MALLORY, M. L., J. D. MCLAUGHLIN, AND M. R. FORBES. 2007. Breeding status, contaminant burden and helminth parasites of Northern Fulmars *Fulmarus glacialis* from the Canadian high Arctic. Ibis 149: 338–344.

MAXWELL, M. H. 1987. The avian eosinophil: a review. Worlds Poultry Science Journal 43:190–207.

MAXWELL, M. H. AND G. W. ROBERTSON. 1998. The avian heterophil leucocyte: a review. Worlds Poultry Science Journal 54:155–178.

MILES, J. A. R. AND M. C. P. STOKER. 1948. Puffinosis, a virus epizootic of the Manx Shearwater (*Puffinus p. puffinus*). Nature 161:1016–1017.

MILES, J. A. R. AND M. C. P. STOKER. 1953. A disease of Manx Shearwaters: further observations in the field. Journal of Animal Ecology 22:123–133.

MINGUEZ, E. 1996. The incidence of injuries on the feet of Storm-Petrels *Hydrobates pelagicus* in Cantabria, northern Spain. Alauda 64:449–450.

MORSE, D. H. AND C. W. BUCHEISTER. 1977. Age and survival of breeding Leach's Storm-Petrels in Maine. Bird Banding 48:341–349.

NUTTALL, P. A., C. M. PERRIS, AND K. A. HARRAP. 1982. Further studies on puffinosis, a disease of the Manx Shearwater (*Puffinus puffinus*). Canadian Journal of Zoology 60:3462–3465.

OSAWA, H. R. C., R. C. SUMMERBELL, K. V. CLEMONS, T. KOGA, Y. P. RON, A. RASHID, P. G. SOHNLE, D. A. STEVENS, AND R. TSUBOI. 1998. Dermatophytes and the host defense. Medical Mycology 36:S166–S173.

OTS, I. AND P. HÕRAK. 1998. Health impact of blood parasites in breeding Great Tits. Oecologia 116:441–448.

OTS, I., A. MURUMÄGI, AND P. HÕRAK. 1998. Haematological health state indices of reproducing Great Tits: methodology and sources of natural variation. Functional Ecology 12:700–707.

OWEN, J. C. 2011. Collecting, processing, and storing avian blood: a review. Journal of Field Ornithology 82:339–354.

QUILLFELDT, P., P. A. R. MCGILL, R. W. FURNESS, E. MÖSTL, K. LUDYNIA, AND J. F. MASELLO. 2012. Impact of miniature geolocation loggers on a small petrel, the Thin-billed Prion *Pachyptila belcheri*. Marine Biology 159:1809–1816.

ROSE, E. M., P. HESKETH, AND B. M. OGILVIE. 1979. Peripheral blood leukocyte response to coccidial infection: a comparison of the response in rats and chickens and its correlation with resistance to reinfection. Immunology 36:71–79.

SALVANTE, K. G. 2006. Techniques for studying integrated immune function in birds. Auk 123:575–586.

SCOTT, D. A. 1970. The breeding biology of the Storm-Petrel. Thesis. University of Oxford, UK.

THRELFALL, W. 1969. Anomalous conditions in three species of birds. Canadian Field-Naturalist 83:384–388.

THRELFALL, W. 1974. Foot injuries in Leach's Storm-Petrels. Wilson Bulletin 86:65–67.

WATERS, W. E. 1964. Observations on small petrels at St. Kilda, 1961-62. Scottish Birds 3:73–81.

ZAR, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New York, USA.

ZAVALAGA, C. B., S. D. EMSLIE, F. A. ESTELA, M. S. MÜLLER, G. DELL'OMO, AND D. J. ANDERSON. 2012. Overnight foraging trips by chick-rearing Nazca Boobies *Sula granti* and the risk of attack by predatory fish. Ibis 154:61–73.

ZINK, R. M. AND J. L. ELDRIDGE. 1980. Why does Wilson's Petrel have yellow on the webs of its feet? British Birds 73:385–387.