

Offspring innate immunity varies with parental age in a long-lived seabird

Beatrice Berardi^{a,b,*}, Gianluca Damiani^{a,b}, Gábor Á. Czirják^c, Silvia Filippi^a, Giacomo Dell'Omo^b, David Costantini^{a,b}

^a Department of Ecological and Biological Sciences, University of Tuscia, Largo dell'Università s.n.c., 01100 Viterbo, Italy

^b Ornis italica, piazza Crati, 15, 00199 Rome, Italy

^c Department of Wildlife Diseases, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany

ARTICLE INFO

Keywords:

Ageing
Parental effects
Seabirds
Oxidative stress
Immunity
shearwater
Linosa

ABSTRACT

Parental age at reproduction is increasingly recognized as a factor influencing offspring lifespan and other fitness-related traits, yet the underlying proximate physiological mechanisms remain poorly understood. Immune function and oxidative status are two potential mediators of age-related parental effects, as both are key hallmarks of ageing. However, very few studies have examined the relationship between parental age and offspring physiological condition in wild populations. We examined immunological and cellular mechanisms potentially responsible for parental age effects in the long-lived seabird Scopoli's shearwater (*Calonectris diomedea*). We measured 10 markers of immune function and oxidative status in 35 chicks from either younger or older parents at two different developmental phases: one month of age and at fledging. Chicks of younger parents exhibited higher haptoglobin levels at fledging compared to chicks of older parents. No effects of parental age were found on leukocyte profiles, humoral components of acquired immunity, antioxidant enzyme activity, or DNA damage in the offspring. Our results suggest, whilst chicks of younger parents might experience more stressful conditions, overall mechanisms supporting somatic maintenance might shield offsprings from the transgenerational transfer of molecular damage that parents accumulate with age. Our findings provide novel insights into the physiological bases of parental age effects in a long-lived species.

1. Introduction

Parental effects refer to phenotypic influences on offspring that arise independently of genotype (Kilner et al., 2015). These effects can be mediated through behaviour, epigenetic modifications, or physiological factors transmitted from parents to offspring (Badyaev and Uller, 2009). One key determinant of parental effects is the age of the individuals (Hecht, 2021). Age can lead to significant changes in organismal biology, particularly at the physiological and behavioral levels, with important consequences for reproductive investment and, as a result, for offspring fitness (Lemaître and Pavard, 2024; Walsh et al., 2024). Studies investigating the impact of parental age on offspring fitness have yielded contrasting results. Depending on the species and the ecological or environmental context, older parents generate either higher-quality (e.g., wild yellow-bellied marmots *Marmota flaviventris* in Kroeger et al., 2020; nematode *Caenorhabditis elegans* in Travers et al., 2021) or lower-quality offspring (e.g., house sparrows *Passer domesticus* in Schroeder et al., 2015; multiple species reviewed in Monaghan et al.,

2020). Despite these findings, the physiological mechanisms through which parental age influences offspring fitness remain poorly understood. Studies on laboratory and domestic species (Wang and vom Saal, 2000; Sparks et al., 2020) suggest that age-related hormonal and immunological changes in parents can be transmitted to offspring, significantly influencing their physiology and development. Studies on wild birds also found parental age-related effects on immune traits, although there is no agreement between studies on different species. In free-living tree swallows (*Tachycineta bicolor*), adult females experience immunosenescence (the deterioration of the immune function with age; Pawelec, 2018), which negatively affects offspring growth (Palacios et al., 2011). By contrast, in house wrens (*Troglodytes aedon*), offspring immune response to an antigen challenge increased with maternal age (Bowers et al., 2017).

Oxidative stress-related factors can also be inherited by the offspring (Romero-Haro and Alonso-Alvarez, 2020). Oxidative stress, a cellular imbalance between the generation of reactive oxygen species (ROS) and antioxidant defenses that results in different rates of molecular oxidative

* Corresponding author at: Department of Ecological and Biological Sciences, University of Tuscia, Largo dell'Università s.n.c., 01100 Viterbo, Italy.

E-mail address: beatrice.berardi@unitus.it (B. Berardi).

damage, is particularly relevant because it can potentially compromise the individual survival or reproductive perspectives (Costantini and Verhulst, 2009; Halliwell and Gutteridge, 2015; Costantini, 2024). Despite the well-established role of oxidative stress in several age-related physiological conditions, to the best of our knowledge the effect of parental age on offspring oxidative status has never been investigated in natural animal populations. This is an important knowledge gap to fill to advance our understanding of the mechanisms underlying the influence of parental age on offspring.

In this cross-sectional study, we investigated whether age-related parental effects are mediated by immunological and cellular mechanisms in a long-lived seabird, the Scopoli's shearwater (*Calonectris diomedea*). This species exhibits three key traits that make it an ideal model for this type of analysis: females lay only one egg per year, so there is no sibling competition; both parents equally share incubation and chick-rearing duties; and pairs are monogamous (Dell'Omo, 2020). Specifically, we analysed 10 markers to evaluate oxidative status and immune function in offspring in relation to parental age. These included two antioxidants (SOD, GPx) and DNA damage as indicators of oxidative status. To assess immune function, we measured both cellular (leucocyte counts) and humoral (immunoglobulin Y and haptoglobin) effectors of innate and adaptive immunity.

Based on previous studies on ageing in long-lived seabirds (e.g., Lecomte et al., 2010; Herborn et al., 2016; Xia and Møller, 2018), we expected similar levels of physiological markers in offspring of older and younger parents if the species invests heavily in somatic maintenance throughout life. Alternatively, if older individuals undergo immunosenescence and experience a decline in antioxidant defenses, and if this ageing signature is transmitted to their offspring, we would expect lower levels of markers in the progeny of older parents.

2. Materials & methods

2.1. Study population and data sampling

We carried out the work on a population of Scopoli's shearwaters breeding on Linosa island, located in South Western Mediterranean Sea (35°52' N, 12°52' E). During the 2024 breeding season, we collected blood samples from 19 chicks from older parents (both parents within the age range 17–22) and from 16 chicks from younger parents (both parents within the age range 6–10), respectively. Sampling was carried out when chicks were 1 month old and replicated near fledging when 80 days old, to assess whether parental effects depended on developmental phase. In total, we collected 61 samples because we sampled 25 chicks at both phases of development and 11 at one of the two phases. Chicks of the two age groups were similar for body mass or metrics of body size (beak length and beak thickness) in both phases of development (p -value ≥ 0.147). This result is consistent with the findings from the analysis of a larger dataset (Berardi et al., 2025, under review). To identify the age groups, we first determined the age of parents based on ringing history. Second, we selected the pairs following two criteria. The first criterion was the age structure of the population. Individuals were classified as younger if they were breeding for the first time, which typically occurs at around 6 years of age. Older individuals were defined as those in the 17–22 year age range.

The second criterion concerned the age difference between the two parents. Since mating in this species is not age-assortative and age gaps between partners can be substantial, we only included pairs in which the age difference between partners did not exceed 2 years for the younger pairs, and 5 years for the older pairs.

At both samplings, we collected 300 μ l of blood from the tarsal vein. The blood was straightaway transferred into heparinized tubes and stored in a cool box until centrifugation (which occurred within max. Two hours). A drop of blood of each sample was smeared onto a glass microscope slide for leucocyte counts. Blood samples were centrifuged for 5 min (1177 g) to separate the plasma from red blood cells and then

stored at -80°C at the laboratory facilities until analyses.

2.2. Quantification of blood-based markers

Following established protocols (e.g. Costantini et al., 2013; Cheron et al., 2022), we measured the activity of two antioxidant enzymes, Superoxide Dismutase (SOD) ($N = 57$) and Glutathione Peroxidase (GPx) (both expressed as units/mg of proteins) ($N = 57$) using the RANSOD and RANSEL assays (Randox Labs., Crumlin, UK), respectively. In addition to assessing antioxidant activity, we measured nuclear DNA damage in cells ($N = 47$) using the Comet assay (single-cell gel electrophoresis), which quantifies the length of DNA strand breaks (in μm) (Giovani et al., 2022).

To assess the immune function of each chick we also relied on validated methods (e.g. Messina et al., 2025; Reinoso-Pérez et al., 2025). Briefly, we determined (i) the plasma concentration of haptoglobin (in mg/ml) ($N = 53$) using the commercial kit “PHASE”™ Haptoglobin Assay (Tridelta, Ireland), (ii) the plasma concentration of immunoglobulin Y (IgY, in optical density (OD)) ($N = 57$) using an in-house ELISA with commercial anti-chicken antibodies, and (iii) the leucocyte profile, assessed by counting the different types of white blood cells (WBCs) using blood smears prepared in the field ($N = 51$) and stained with Wright-Giemsa Stain Solution (Reinoso-Pérez et al., 2025; Prüter et al., 2020). Smears were examined under a microscope at 100 $\times$ magnification using oil immersion, and the relative number and types of leucocytes were determined by counting 100 leucocytes per smear. The number of white blood cells of each type was expressed per 10⁴ red blood cells (RBCs) (Prüter et al., 2020). All measurements were performed in duplicate, and the mean of each duplicate was included in the statistical models.

2.3. Statistical analyses

We fitted Generalized Linear Mixed Effect Models (GLMMs) with R package *lme4* (v. 1.1.36, Bates et al., 2015) to test the effect of parental age on physiological metrics measured in their offspring. In each model, we entered parental age (older vs. younger) and developmental phase (DP, 1-month old vs. near fledging) as a two-level fixed effect factor; the interaction between parental age and developmental phase as a fixed factor; body mass of chicks as a covariate since it is a proxy for sex-related differences (female Scopoli's shearwater chicks are smaller than males at fledging, Karris et al., 2013); and chick identity as random factor because for some chicks ($N = 26$) we had measures at both developmental phases. Random effects were removed from models in which their estimated variance was zero. To meet the assumptions of the GLMMs, we used: (i) a Gamma family with a log-link function for SOD, GPx, and haptoglobin; (ii) a Gaussian family with an identity-link function for COMET and IgY; (iii) negative binomial family GLMMs for heterophils, eosinophils, basophils, lymphocytes and monocytes count. To check for collinearity, we calculated the variance inflation values (VIF). VIF were below 5 for models of GPx, DNA damage, haptoglobin, IgY, heterophils, eosinophils, basophils, and lymphocytes, indicating negligible collinearity among predictors. VIF was higher than 5 but less than 10 for SOD and monocytes, indicating moderate collinearity. Dropping of scaled body mass from the models reduced the collinearity, but results were unchanged, indicating that collinearity did not influence the statistical outcomes.

When we had a significant interaction, we explored it running specific post-hoc comparisons using the package *pbrtest* (v. 0.5.3, Halekoh and Højsgaard, 2014).

3. Results

We found significant differences in haptoglobin levels of chicks depending on parental age and developmental phase (Table 1), regardless of their body mass. Specifically, post-hoc comparisons

Table 1

Outcomes of GLMMs fitted to test effect of parental age (younger vs. older pair) and chick developmental phase (1-month old vs. fledging) on three oxidative status markers and five immune markers in the offspring. Significant variables are shown in bold, and standard errors for each estimated parameter are given in parentheses. Hapto: Haptoglobin, Eos: Eosinophils, Heter: Heterophils, Lymph: Lymphocytes, Bas: Basophils, Mono: Monocytes, SD: Standard Deviation. Fixed effects: parental age, developmental phase; Random effects: chick identity. Random effects were removed from models in which their estimated variance was zero. Statistical significance is reported as follows: 0 ‘***’, 0.001 ‘**’, 0.05 ‘*’, 0.1, ‘.’.

Oxidative status	SOD	GPX	DNA damage
(Intercept)	0.762*** (0.143)	−2.549*** (0.211)	14.438*** (1.763)
Younger pair	−0.187 (0.189)	0.020 (0.270)	−0.136 (2.220)
Fledging period	−0.642** (0.186)	−0.257 (0.281)	1.638 (2.562)
Chick body mass	−0.027 (0.110)	−0.193 (0.153)	1.511 (1.197)
Younger pair × Fledging period	0.217 (0.158)	0.084 (0.263)	1.926 (2.668)
SD (Intercept ring)	0.272	0.318	1.999
SD (Observations)	0.281	0.407	4.270
Variance of fixed effects	0.353	0.254	0.229
Variance of random effects	0.673	0.551	0.368

Immunity	IgY	Hapto	Eos	Heter	Lymph	Bas	Mono
(Intercept)	0.244*** (0.025)	−0.089 (0.189)	1.668*** (0.352)	3.715*** (0.129)	3.935*** (0.112)	0.886 (1.039)	−1.140* (0.538)
Younger pair	0.026 (0.032)	−0.226 (0.242)	−0.041 (0.434)	−0.090 (0.155)	0.117 (0.140)	−0.351 (1.271)	0.120 (0.665)
Fledging period	0.004 (0.034)	−0.773** (0.249)	0.182 (0.593)	−0.103 (0.226)	−0.142 (0.191)	0.865 (1.757)	3.149*** (0.662)
Chick body mass	0.024 (0.017)	0.128 (0.140)	−0.015 (0.263)	−0.094 (0.101)	0.114 (0.084)	−0.775 (0.781)	−0.595 (0.360)
Younger pair × Fledging period	−0.019 (0.034)	0.762** (0.224)	−0.309 (0.586)	0.112 (0.220)	−0.061 (0.188)	0.709 (1.718)	−0.895 (0.519)
SD (Intercept ring)	0.048	0.324	–	–	–	–	1.109
SD (Observations)	0.054	0.385	–	–	–	–	–
Variance of fixed effects	0.083	0.209	–	–	–	–	0.402
Variance of random effects	0.486	0.550	–	–	–	–	0.919

revealed that, near fledging, chicks from younger parents had significantly higher haptoglobin levels ($+ 0.54 \pm 0.21$ mg/ml, $p = 0.01$; Fig. 1a) than those born to older parents. In contrast, regardless of developmental phase, chicks from both younger and older parents exhibited similar levels of SOD, GPx, and DNA damage (Table 1 and Fig. 2), as well as comparable IgY concentrations (Fig. 1a) and leucocyte profile (Table 1 and Fig. 1). Only two markers - SOD concentration and the number of monocytes - showed variation in relation to developmental phase (Table 1). In particular, 1 month old chicks had significantly higher SOD (Fig. 2a) and lower monocyte counts (Fig. 1f) compared to chicks close to fledging.

4. Discussion

The results of our study show that Scopoli's shearwater chicks from younger parents had higher haptoglobin levels at fledging compared to chicks from older parents. Considering the developmental period, chicks from both younger and older parents had similar levels of haptoglobin at one month of age. By contrast, near fledging, chicks of older parents had lower levels of haptoglobin than chicks of younger parents, possibly indicating a lower synthesis of this protein. Haptoglobin is an acute-phase protein involved in the induced innate immune response (Andersen et al., 2017). Haptoglobin circulates in the blood at low concentrations, but its levels increase rapidly in response to infections, inflammation, or stress (Hörak et al., 2003; Matson et al., 2012). Given the physiological roles of haptoglobin, our results suggest that chicks of younger parents might cope with stressful conditions that persist throughout their development, which do not appear to be related to oxidative stress, as SOD levels decrease during the pre-fledging period.

Several studies have shown that diet composition significantly influences innate immunity indices, independently of food limitation (Berghof et al., 2013; Nwaogu et al., 2020). For example, in laying hens, the use of feed additives led to stress-relaxation effects, accompanied by a decrease in circulating haptoglobin (Park and Kim, 2015). In another experimental study on chickens, gastrointestinal inflammatory disorders induced an intense acute-phase protein response, including haptoglobin (Georgieva et al., 2010). Similar results have been observed in free-living common bulbuls (*Pycnonotus barbatus*), for which the inflammatory response increased under specific nutrient limitations (Nwaogu et al., 2020). Based on these studies, one explanation for our results might lie in the nutritional status of chicks, mediated by differences in parental foraging behaviour associated with age and experience. Younger and inexperienced seabirds are less efficient at feeding their chicks than older, experienced individuals. They tend to forage in less-productive areas, and their chicks are fed a higher proportion of prey items with low energy content (Limmer and Becker, 2009; Haug et al., 2015). Moreover, in our study area, fishing activities strongly influence the foraging behaviour of shearwaters, with younger individuals tending to interact more frequently with fishing vessels, especially during the late chick-rearing phase (Cianchetti-Benedetti et al., 2018; Cortés et al., 2018). These interactions can facilitate access to demersal fish, which are potentially less nutritious than shearwaters' natural prey (small fish, squid, and crustaceans). It is therefore possible that younger parents raise their chicks under suboptimal food conditions, triggering physiological stress, which in turn induces an inflammatory response. A specific analysis of diet quality in relation to parental age and foraging behaviour could clarify these aspects.

Our results also highlight the need to consider the intense stress that

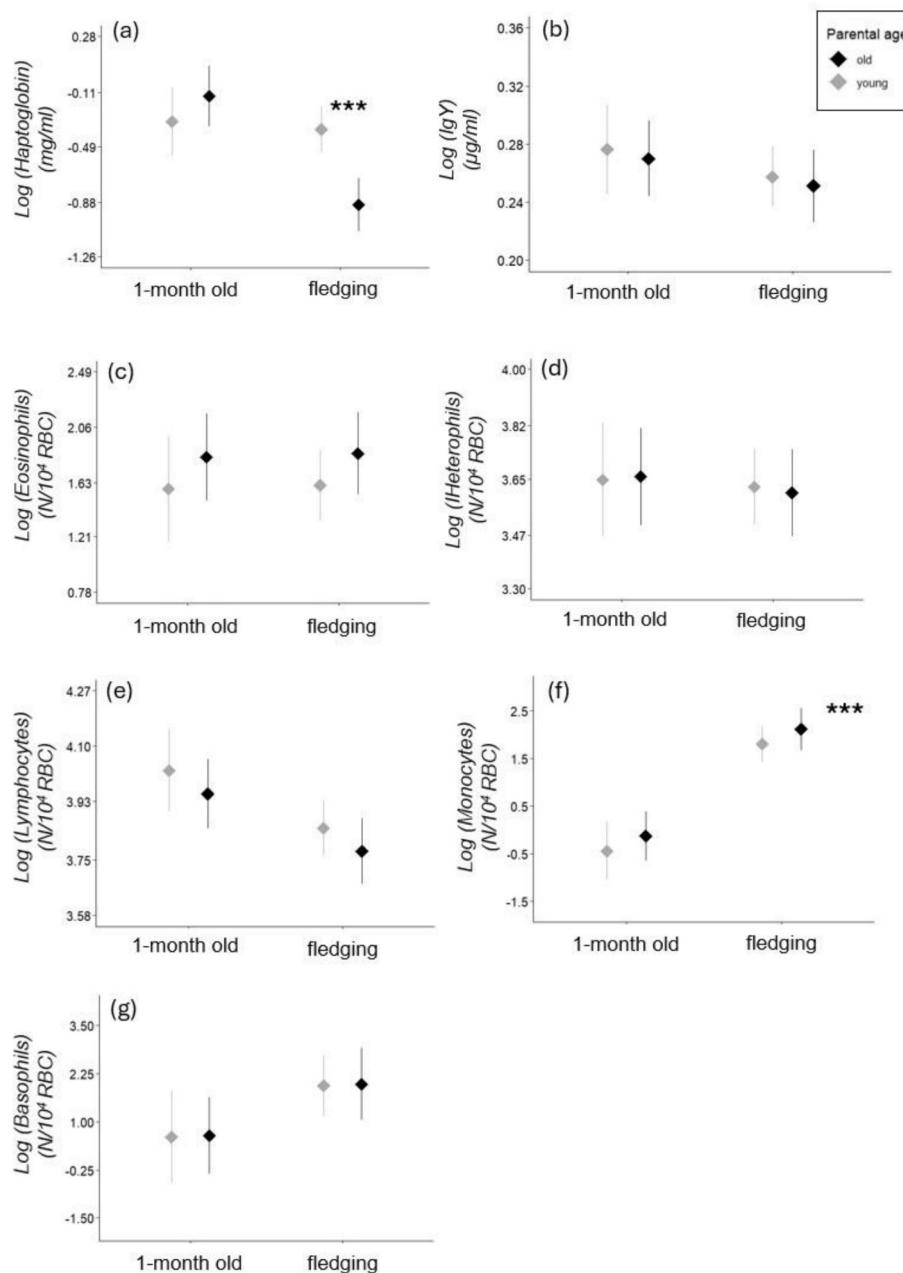


Fig. 1. Levels of Haptoglobin (a), IgY (b), eosinophils (c), heterophils (d), lymphocytes (e), monocytes (f) and basophils (g) in offspring of Scopoli's shearwaters in relation to parental age (younger vs. older) and developmental phase (DP, 1-month old vs. near fledging). Values (on the log scale) are presented as estimated marginal means $\pm$ standard errors. Statistical significance is reported as follows: 0 '***', 0.001 '**', 0.05 '*', ' 0.1, "1.

seabird chicks undergo during the fledging period (Corbel et al., 2010). At this stage, the depletion of energy reserves due to fasting (Ramos et al., 2003) and the increased metabolic activity of skeletal muscles caused by wing-flapping behaviour in preparation for flight (Yoda et al., 2017) can amplify stress levels. Differential activation of metabolic stress-response pathways - such as haptoglobin synthesis - may occur between chicks of younger and older parents (Bertaglia et al., 2014). Therefore, immune function during the pre-fledging period may represent a key target of natural selection, as indicated by the increase in monocytes occurring during this period compared to the early stages of chick development, with parental age potentially amplifying or mitigating the strength of this selective pressure. Further studies are needed to investigate these hypotheses, particularly concerning the link between poor nutrition, loss of body mass during the fasting period, and inflammation. Finally, we found that haptoglobin level was not

significantly influenced by the body mass of chicks at fledging, which is consistent with findings from other studies on seabirds (Berrow et al., 2000; Jones et al., 2014).

We did not find any relationships between parental age and cell counts, IgY, antioxidant enzymes, or DNA damage of offspring in both phases of development. In long-lived species, older breeders are expected to maintain robust somatic condition, with cellular processes that support immune function and reduce oxidative stress, ensuring resources remain available for reproduction (Bichet et al., 2022; Lecomte et al., 2010; Xia and Møller, 2018). Mechanisms of sustained somatic maintenance might reduce phenotypic differences between younger and older parents during reproduction. In so doing, they might limit the impact of parental age on offspring to dietary differences related to the foraging experience. For instance, in previous work, we found that older breeding adult shearwaters have higher levels of antioxidant enzymes

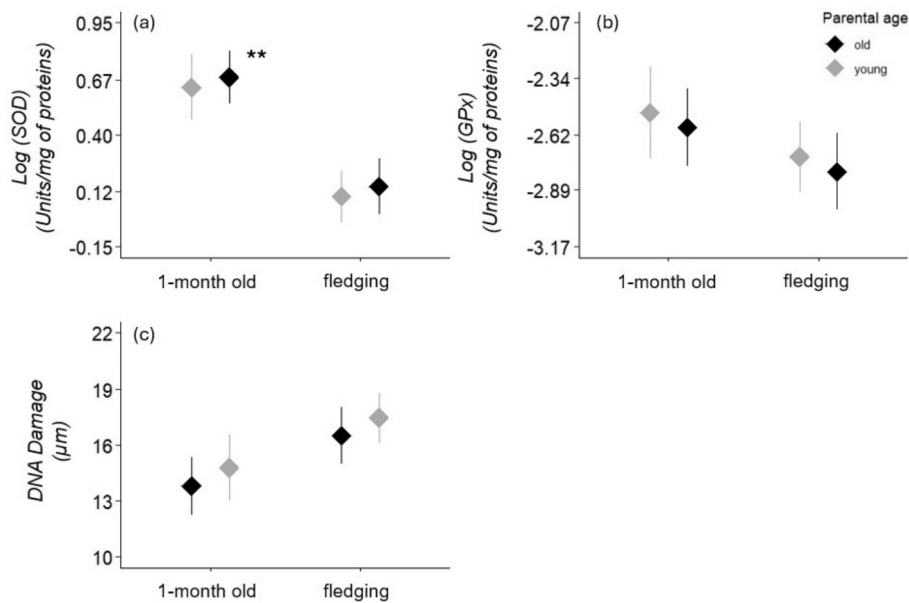


Fig. 2. Levels of SOD (a), GPx (b), and DNA damage (c) in offspring of Scopoli's shearwaters in relation to parental age (younger vs. older) and developmental phase (DP, 1-month old vs. near fledging). Values (on the log scale for SOD and GPx) are presented as estimated marginal means $\pm$ standard errors.

and markers of acquired immunity than younger breeding adult shearwaters (Berardi et al., 2025).

5. Conclusions

In conclusion, our results indicate that parental age has a limited influence on the oxidative status and immune function of their offspring, which is in line with other studies on long-lived species. Further studies are needed to unravel the mechanisms that drive the difference in haptoglobin between offspring of young and older parents. We propose that this difference in haptoglobin might be due to differences in food quality or quantity, potentially driven by an interaction between parental age and foraging efficiency. Our findings provide new insights into age-related parental effects on the physiological condition of offspring in a long-lived species.

Ethic statement

Fieldwork was carried out under the authorizations issued by the Regione Siciliana, Assessorato Agricoltura e Foreste with letter Prot. 17,233 dated December 1, 2010, and subsequent communications Prot. 2452 dated February 01, 2018, and Prot. 48,759 dated May 22, 2023.

CRediT authorship contribution statement

Beatrice Berardi: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Gianluca Damiani:** Writing – review & editing, Methodology. **Gábor Á. Cziráj:** Writing – review & editing, Validation, Resources, Methodology, Data curation. **Silvia Filippi:** Writing – review & editing, Validation, Resources, Methodology, Data curation. **Giacomo Dell’Omo:** Writing – review & editing, Validation, Supervision, Resources, Conceptualization. **David Costantini:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Conceptualization.

Significance statement

Parental age at reproduction can influence multiple offspring fitness-related traits. However, the proximate physiological mechanisms underlying age-related parental effects in wild populations remain poorly

understood, as most evidence comes from captive animals that may not reflect natural ecological conditions. Understanding the physiological bases of these effects is key to advancing our knowledge of how parental ageing phenotypes are transmitted across generations.

In this study on a long-lived seabird species, we show that parental age influences offspring innate immunity, while no effects are detected on acquired immunity or oxidative status. These findings raise important considerations about the hallmarks of long-lived species, including their potential to buffer offspring from the negative effects of parental ageing, and the parental age-related factors that, in contrast, may contribute to variation in chicks' innate immunity.

By integrating multiple physiological markers, our work highlights the value of mechanistic approaches to studying age-related parental effects. Moreover, it represents one of the few comparative models exploring both immune and oxidative markers in the offspring of a long-lived species, offering a new perspective on the physiological mechanisms linking parental age to offspring phenotype.

Funding statement

This study was funded by a doctoral fellowship from the University of Tuscia to B-B and from the association Ornithologica. Field work was financially supported by *Ornithologica* and *Berta maris*.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgments

We thank Agustina Gómez-Laich and Eleonora Dell’Omo for their support in the field, and Katja Pohle for technical support during laboratory analyses. We are very grateful to Emma Valeri, Elena Paccosi and Diletta Guzzon for their support and assistance throughout the laboratory analyses, especially in performing the comet assay. Finally, we also thank two anonymous reviewers for providing constructive comments that helped us to improve the presentation of our work.

Data availability

Data will be made available on request.

References

- Andersen, C.B.F., Stødtkilde, K., Sæderup, K.L., Kuhlee, A., Raunser, S., Graversen, J.H., Moestrup, S.K., 2017. Haptoglobin. *Antioxid. Redox Signal.* 26, 814–831. <https://doi.org/10.1089/ars.2016.6793>.
- Badyaev, A.V., Uller, T., 2009. Parental effects in ecology and evolution: mechanisms, processes and implications. *Philos. Trans. R. Soc. B* 364, 1169–1177. <https://doi.org/10.1098/rstb.2008.0302>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Berardi, B., Dell'Omo, G., Damiani, G., et al., 2025. Age-related changes of oxidative status and immune function in a long-lived seabird. *Authorea*. <https://doi.org/10.22541/au.175686843.34545156.v1>.
- Berghof, T.V.L., Parmentier, H.K., Lammers, A., 2013. Transgenerational epigenetic effects on innate immunity in broilers: an underestimated field to be explored? *Poult. Sci.* 92, 2904–2913. <https://doi.org/10.3382/ps.2013-03177>.
- Berrow, S.D., Humpidge, R., Croxall, J.P., 2000. Influence of adult breeding experience on growth and provisioning of Wandering Albatross *Diomedea exulans* chicks at South Georgia. *Ibis* 142, 199–207. <https://doi.org/10.1111/j.1474-919X.2000.tb04859.x>.
- Bertaggia, E., Scabia, G., Dalise, S., Lo, Verso F., Santini, F., Vittori, P., Chisari, C., Sandri, M., Maffei, M., 2014. Haptoglobin is required to prevent oxidative stress and muscle atrophy. *PLoS One* 9, 1–15. <https://doi.org/10.1371/journal.pone.0100745>.
- Bichet, C., Moiron, M., Matson, K.D., Vedder, O., Bouwhuis, S., 2022. Immunosenescence in the wild? A longitudinal study in a long-lived seabird. *J. Anim. Ecol.* 91, 458–469. <https://doi.org/10.1111/1365-2656.13642>.
- Bowers, E.K., Sakaluk, S.K., Thompson, C.F., 2017. Interactive effects of parental age on offspring fitness and age-assortative mating in a wild bird. *J. Exp. Zool. A Ecol. Integr. Physiol.* 327, 302–310. <https://doi.org/10.1002/jez.2090>.
- Cheron, M., Costantini, D., Angelier, F., Ribout, C., Brischoux, F., 2022. Aminomethylphosphonic acid (AMPA) alters oxidative status during embryonic development in an amphibian species. *Chemosphere* 287, 1–32. <https://doi.org/10.1016/j.chemosphere.2021.131882>.
- Cianchetti-Benedetti, M., Dell'Omo, G., Russo, T., Catoni, C., Quillfeldt, P., 2018. Interactions between commercial fishing vessels and a pelagic seabird in the southern Mediterranean Sea. *BMC Ecol.* 18, 54. <https://doi.org/10.1186/s12898-018-0212-x>.
- Corbel, H., Geiger, S., Groscolas, R., 2010. Preparing to fledge: the adrenocortical and metabolic responses to stress in king penguin chicks. *Funct. Ecol.* 24, 82–92. <https://doi.org/10.1111/j.1365-2435.2009.01619.x>.
- Cortés, V., García-Barcelona, S., González-Solís, J., 2018. Sex-and age-biased mortality of three shearwater species in longline fisheries of the Mediterranean. *Mar. Ecol. Prog. Ser.* 588, 229–241. <https://doi.org/10.3354/meps>.
- Costantini, D., 2024. The long and the short of it: How oxidative stress drives cellular senescence, ageing, and lifespan of animals. In: *The Role of Organismal Oxidative Stress in the Ecology and Life-History Evolution of Animals*. Cham, Springer Nature Switzerland, pp. 369–418.
- Costantini, D., Verhulst, S., 2009. Does high antioxidant capacity indicate low oxidative stress? *Funct. Ecol.* 23, 506–509. <https://www.jstor.org/stable/40205558>.
- Costantini, D., Monaghan, P., Metcalfe, N., 2013. Loss of integration is associated with reduced resistance to oxidative stress. *J. Exp. Biol.* 216, 2213–2220. <https://doi.org/10.1242/jeb.083154>.
- Dell'Omo, G., 2020. In: Danaus (Ed.), *State of the Knowledge on the Scopoli Shearwater *Calonectris diomedea* Breeding on Linosa Island (Pelagic Archipelago, Sicilian Channel), Life on Island. Biodiversity in Sicily and Surrounding Islands*, pp. 331–338.
- Georgieva, T.M., Koinarski, V.N., Urumova, V.S., Marutsov, P.D., Christov, T.T., Nikolov, J., Koinarski, Z.V., 2010. Effects of *Escherichia coli* infection and *Eimeria tenella* invasion on blood concentrations of some positive acute phase proteins (haptoglobin (PIT 54), fibrinogen and ceruloplasmin) in chickens. *Rev. Med. Vet.* 161, 84–89.
- Giovani, G., Filippi, S., Molino, C., Peruffo, A., Centelleghé, C., Meschini, R., Angeletti, D., 2022. Plastic additive di (2-ethylhexyl) phthalate (DEHP) causes cell death and micronucleus induction on a bottlenose dolphin's (*Tursiops truncatus*) in vitro-exposed skin cell line. *Front. Mar. Sci.* 9, 1–12. <https://doi.org/10.3389/fmars.2022.958197>.
- Halekoh, U., Højsgaard, S., 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbrtest. *J. Stat. Softw.* 59, 1–30. <https://www.jstatsoft.org/v59/i09/>.
- Halliwell, B., Gutteridge, J.M.C., 2015. *Free Radicals in Biology and Medicine*, 5th ed. Oxford University Press.
- Haug, F.D., Paiva, V.H., Werner, A.C., et al., 2015. Foraging by experienced and inexperienced cory's shearwater along a 3-year period of ameliorating foraging conditions. *Mar. Biol.* 162, 649–660. <https://doi.org/10.1007/s00227-015-2612-1>.
- Hecht, L., 2021. The importance of considering age when quantifying wild animals' welfare. *Biol. Rev.* 96, 2602–2616. <https://doi.org/10.1111/brv.12769>.
- Herborn, K.A., Daunt, F., Heidinger, B.J., Granroth-Wilding, H.M., Burthe, S.J., Newell, M.A., Monaghan, P., 2016. Age, oxidative stress exposure and fitness in a long-lived seabird. *Funct. Ecol.* 30, 913–921. <https://doi.org/10.1111/1365-2435.12578>.
- Hörak, P., Saks, L., Ots, I., Kullisaar, T., Kollist, H., Zilmer, M., 2003. Physiological effects of immune challenge in captive greenfinches (*Carduelis chloris*). *Can. J. Zool.* 81, 371–379. <https://doi.org/10.1139/z03-020>.
- Jones, M.G.W., Dille, B.J., Hagens, Q.A., et al., 2014. The effect of parental age, experience and historical reproductive success on wandering albatross (*Diomedea exulans*) chick growth and survival. *Polar Biol.* 37, 1633–1644. <https://doi.org/10.1007/s00300-014-1550-6>.
- Karris, G., Thanou, E., Xirouchakis, S., Voulgaris, M.D., Fragedakis-Tsolis, S., Sfenthourakis, S., Giokas, S., 2013. Sex determination of Scopoli's shearwater (*Calonectris diomedea*) juveniles: a combined molecular and morphometric approach. *Waterbirds* 36, 240–246. <https://doi.org/10.1675/063.036.0215>.
- Kilner, R.M., Boncoraglio, G., Henshaw, J.M., Jarrett, B.J., De Gasperi, O., Attisano, A., Kokko, H., 2015. Parental effects alter the adaptive value of an adult behavioural trait. *eLife* 22, 1–25. <https://doi.org/10.7554/eLife.07340>.
- Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M., Martin, J.G.A., 2020. Older mothers produce more successful daughters. *Proc. Natl. Acad. Sci. USA* 117, 4809–4814. <https://doi.org/10.1073/pnas.1908551117>.
- Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Weimerskirch, H., 2010. Patterns of aging in the long-lived wandering albatross. *Proc. Natl. Acad. Sci.* 107, 6370–6375. <https://doi.org/10.1073/pnas.0911811107>.
- Lemaître, J.-F., Pavard, S., 2024. *The Biodemography of Ageing and Longevity*. Cambridge University Press, Cambridge.
- Limmer, B., Becker, P.H., 2009. Improvement in chick provisioning with parental experience in a seabird. *Anim. Behav.* 77, 1095–1101. <https://doi.org/10.1016/j.anbehav.2009.01.015>.
- Matson, K.D., Horrocks, N.P., Versteegh, M.A., Tieleman, B.I., 2012. Baseline haptoglobin concentrations are repeatable and predictive of certain aspects of a subsequent experimentally-induced inflammatory response. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 162, 7–15. <https://doi.org/10.1016/j.cbpa.2012.01.010>.
- Messina, S., Prüter, H., Czirjak, G.A., Costantini, D., 2025. Lower adaptive immunity in invasive Egyptian geese compared to sympatric native waterfowls. *Comp. Biochem. Physiol. A* 299, 1–7. <https://doi.org/10.1016/j.cbpa.2024.111752>.
- Monaghan, P., Maklakov, A.A., Metcalfe, N.B., 2020. Intergenerational transfer of ageing: parental age and offspring lifespan. *Trends Ecol. Evol.* 35, 927–937. <https://doi.org/10.1016/j.tree.2020.07.005>.
- Nwaogu, C.J., Galema, A., Cresswell, W., Dietz, M.W., Tieleman, B.I., 2020. A fruit diet rather than invertebrate diet maintains a robust innate immunity in an omnivorous tropical songbird. *J. Anim. Ecol.* 89, 867–883. <https://doi.org/10.1111/1365-2656.13152>.
- Palacios, M.G., Winkler, D.W., Klasing, K.C., Hasselquist, D., Vleck, C.M., 2011. Consequences of immune system aging in nature: a study of immunosenescence costs in free-living tree swallows. *Ecology* 92, 952–966. <https://doi.org/10.1890/10-0662.1>.
- Park, J.H., Kim, I.H., 2015. Effects of dietary gamma-aminobutyric acid on egg production, egg quality, and blood profiles in layer hens. *Vet. Med.* 60, 629–634. <https://doi.org/10.17221/8531>.
- Pawelec, G., 2018. Age and immunity: what is “immunosenescence”? *Exp. Gerontol.* 105, 4–9. <https://doi.org/10.1016/j.exger.2017.10.024>.
- Prüter, H., Franz, M., Twietmeyer, S., Böhm, N., Middendorff, G., Portas, R., Czirjak, G.A., 2020. Increased immune marker variance in a population of invasive birds. *Sci. Rep.* 10, 1–13.
- Ramos, J.A., Moniz, Z., Solá, E., Monteiro, L.R., 2003. Reproductive measures and chick provisioning of cory's shearwater *Calonectris diomedea borealis* in the Azores. *Bird Study* 50, 47–54. <https://doi.org/10.1080/00063650309461289>.
- Reinos-Pérez, M.T., Dhondt, K.V., Yáñez Abad, A.A., Rodríguez-García, V.M., Dhondt, A.A., 2025. Pathogen-induced stress in wild house finches (*Haemorrhous mexicanus*): leukocyte dynamics as health indicators. *J. Wildlife Dis.* 61, 334–347. <https://doi.org/10.7589/JWD-D-24-00164>.
- Romero-Haro, A.A., Alonso-Alvarez, C., 2020. Oxidative stress experienced during early development influences the offspring phenotype. *Am. Nat.* 196, 704–716. <https://doi.org/10.1086/711399>.
- Schroeder, J., Nakagawa, S., Rees, M., Mannarelli, M.E., Burke, T., 2015. Reduced fitness in progeny from old parents in a natural population. *Proc. Natl. Acad. Sci.* 112, 4021–4025. <https://doi.org/10.1073/pnas.1422715112>.
- Sparks, A.M., Hayward, A.D., Watt, K., Pilkington, J.G., Pemberton, J.M., Johnston, S.E., McNeilly, T.N., Nussey, D.H., 2020. Maternally derived anti-helminth antibodies predict offspring survival in a wild mammal. *Proc. R. Soc. B* 287, 1–9. <https://doi.org/10.1098/rspb.2020.1931>.
- Travers, L.M., Carlsson, H., Lind, M.I., Maklakov, A.A., 2021. Beneficial cumulative effects of old parental age on offspring fitness. *Proc. R. Soc. B* 288, 1–10. <https://doi.org/10.1098/rspb.2021.1843>.
- Walsh, M.R., Christian, A., Feder, M., Korte, M., Tran, K., 2024. Are parental condition transfer effects more widespread than is currently appreciated? *J. Exp. Biol.* 227, 1–9. <https://doi.org/10.1242/jeb.246094>.
- Wang, M.H., vom Saal, F., 2000. Maternal age and traits in offspring. *Nature* 407, 469–470. <https://doi.org/10.1038/35035156>.
- Xia, C., Möller, A.P., 2018. Long-lived birds suffer less from oxidative stress. *Avian Res.* 9, 1–7. <https://doi.org/10.1186/s40657-018-0133-6>.
- Yoda, K., Shiozaki, T., Shirai, M., Matsumoto, S., Yamamoto, M., 2017. Preparation for flight: pre-fledging exercise time is correlated with growth and fledging age in burrow-nesting seabirds. *J. Avian Biol.* 48, 881–886. <https://doi.org/10.1111/jav.01186>.