

and antibody response to vaccination. In addition, the overall effect size for associations between sleep duration and antibody response to vaccination in women did not reach statistical significance. This is in contrast to men where a large effect size was observed. That these biologic factors were determined in this meta-analysis to contribute to effect sizes for associations between short sleep duration and antibody responses to vaccination is important because age and sex are host-related factors known to contribute to vaccine effectiveness based on many studies that did not include sleep measures. As such, the findings of this meta-analysis corroborate extant literature and suggest that associations between short sleep duration and antibody response to vaccination are real.

That only seven studies conducted during the last 20 years met inclusion criteria for the Spiegel *et al.*⁷ meta-analysis presents an opportunity for critical public health research focused on sleep and its role in vaccine effectiveness. Although effective vaccines and vaccination programs for SARS-CoV-2 top the current list of global health needs, the World Health Organization lists additional priority diseases for research¹⁷. In addition to COVID-19, the deadliest communicable diseases on this list include ebola virus disease (~50% fatality rate), Lassa fever (~15% fatality rate in hospitalized patients), and Crimean-Congo haemorrhagic fever (~30% fatality rate). The World Health Organization policy recommendations for targeting each of these diseases include vaccine development.

Vaccine development, investment in infrastructure for vaccine deployment, and many other actions are critical in efforts to eradicate vaccine-preventable diseases, as was the case with smallpox. Although additional studies are necessary and many questions remain to be answered, the results of the Spiegel *et al.*⁷ meta-analysis provide convincing evidence that short sleep duration around the time of vaccination reduces antibody responses to vaccination and subsequent protection status. A campaign to inform providers and the public that increasing sleep duration around the time of vaccination can improve vaccine effectiveness appears to be warranted.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Animal behavior: Killer whale mamas' boys

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Long-term study of killer whales reveals that sons stay with their mothers for life, and although this benefits sons, it negatively impacts the mother's reproductive output.

It is an odd but familiar sight in the Pacific waters separating western Canada and the United States (Figure 1):

50-year-old Slick (J16) swims alongside her 31-year-old son, Mike (J26). You will not find a closer mother-son bond in the

animal kingdom. Slick and Mike are Southern resident killer whales, also known as fish-eating resident killer whales, a population that has been studied since the early 1970s. “Resident” is a bit of a misnomer as these whales range widely, but are predictably found in Haro Strait between Canada and the US in the summer months. Mothers and adult sons together — you may not find this that peculiar; after all, we humans maintain lifelong contact with our own offspring, but not for most of the day every day, decade after decade. Among wildlife, such mutual devotion between mother and son, lasting a lifetime, is just not a thing. In fact, mother–adult son association is strikingly rare. In most mammals, males leave the safety of their natal home to seek their fortunes elsewhere¹. In most group-living mammals, mothers and daughters remain together for their lifetimes, forming matrilineal kin groups. But killer whales have taken a different route. Amongst many, but not all, killer whale populations, both sons and daughters stay with the family for life, a pattern known as ‘bisexual philopatry’ (sometimes referred to as social bisexual philopatry, because spatial overlap with other groups is extensive). The question is why? What exactly do Slick and Mike see in each other? A paper in a recent issue of *Current Biology* by Michael Weiss, Darren Croft and colleagues² helps shed light on this intimate bond and unusual social system. The authors examine the costs of sons to maternal reproduction. They suggest that mothers devote a lifetime of care to their sons. This helps make sense of previous work showing that sons cannot survive very well without their mothers: adult mortality increases markedly when the mother dies, especially among sons³.

A lifetime of care? How exhausting. In fact, to demonstrate the cost of sons (more than daughters), Weiss and colleagues² show that sons, but not daughters, inflict biological costs on their mothers’ future reproduction, meaning she has fewer surviving offspring after having sons — and that the more sons a mother had, the greater the effect. This means that sons are costly to mothers and this cost extends late in life, slightly



Figure 1. Orca mother and son.

Mother J16 (left) and son J26 (right). Photo: Center for Whale Research/David Ellifrit, federal research permit NMFS 21238.

increasing as sons age. This is an essential piece of the puzzle, since by definition parental investment in offspring costs investment in other (existing or future) offspring.

Most research on the cost of mammalian parental investment focuses on the period between pregnancy and weaning (cessation of nursing) and rarely considers adulthood. Maternal care is extensive in toothed whales⁴, primates⁵ and elephants⁶. But even with lactation lengths extending to eight years in some species of toothed whale⁷, rivaling the longest lactation periods for great apes⁵, no study has shown lifelong investment in offspring, until now. There is some evidence mothers assist offspring throughout life in primates⁸, although the cost of post-weaning care to maternal reproduction, a necessary component of investment, is often not measured. Rarely do we have lifetime data that allow investigators to examine what it is like to raise sons and daughters well into adulthood and how this impacts the mothers’ reproduction. This is no easy feat unless you are armed with decades of demographic data, as are Weiss and colleagues², who have meticulously tracked the births and deaths of hundreds of individual killer whales for over 50 years. Such longitudinal study is

essential for not only documenting variation in reproduction and survival, but factors that contribute to this variation. In this case, producing sons impacted their mothers’ future reproduction.

But how are killer whale mothers investing in sons? Weiss and colleagues² offer food-sharing as the primary benefit. Killer whales are sexually dimorphic; adult males can weigh twice as much as adult females. Male killer whales may not be as skilled as females at catching salmon because a large body size makes them less maneuverable. Prey-sharing is considered the driving force favoring bisexual philopatry in killer whales⁹. Females are likely more adept at catching prey, especially given the evasive maneuvers of fish¹⁰. If the superior foraging performance of female compared to male killer whales helps explain lifetime maternal investment in sons, is this true for every killer whale population? Nearly everywhere they have been studied, killer whales tend to hunt cooperatively and share prey while specializing on diverse prey that, depending on the population, includes large whales, small cetaceans, pinnipeds, penguins, stingrays, sharks, cephalopods and fish¹¹. Do sons need their mother’s help in feeding

themselves across all populations or just among fish-eating killer whales as Weiss and colleagues² show. The relationships between killer whale feeding strategy, sex differences in hunting efficiency, prey-sharing, maternal care, and social system await further study. Are lifetime mamas' boys borne from a dependency on mamas' hunting skills?

Lifetime association with their mothers may provide other benefits to sons. Older female killer whales serve in a leadership role, which is particularly important when prey is scarce, as older females seem to know where to find prey during hard times, presumably based on long-term memory given the oscillations of prey abundance and scarcity over decades; furthermore, sons follow their mothers more than daughters do¹². Although knowing where to go benefits followers, it doesn't necessarily cost the leader. Whether mothers assist sons in other ways, such as in finding mates, is not entirely clear. But if mothers contribute to their growth, health and survival, that might make sons more attractive to other females, evident by their mating success¹³.

Not only does the study of Weiss and colleagues² help us understand the evolution of killer whale social structure, it also provides insight into mammalian social systems more generally. Extensive maternal care can lead to stability in social structures⁴, which is in line with the observations of killer whales, which have some of the most stable groups (pods) known. Stable groups characterized by bisexual philopatry are seen in other large toothed whales including long-finned pilot whales¹⁴, short-finned pilot whales¹⁵, possibly false killer whales¹⁶, and pygmy killer whales¹⁷. In these species, the relationship between mothers and sons is largely unknown, but genetic data suggests that mating occurs primarily between, rather than within, social groups. This raises several questions regarding how these large, wide-ranging mammals of the sea have evolved to form tight cooperative family groups, while minimizing potentially deleterious costs of inbreeding. Dolphins and whales are a critical comparison group for understanding kinship dynamics in mammalian social systems¹⁸.

Several mysteries remain and call for more long-term studies of individual killer whales at other sites and other delphinid species. Most glaring is the enigma of the extensive post-reproductive lifespan in killer whales and several closely related species¹⁸. Female killer whales cease reproduction in their 40s, but sometimes live into their 80s¹⁹. Several have proposed that post-reproductive lifespan is driven by both reproductive conflict with daughters and extended investment in sons^{3,20}. A long-lived mother promotes the reproductive success of sons and daughters, especially as older sons are more successful than younger ones¹³. In Northern resident killer whales, post-reproductive females were the only ones that consistently shared fish with their adult sons⁹. If the inclusive fitness benefits drive post-reproductive lifespan by reducing reproductive competition with daughters and enhancing sons' fitness, then identifying the costs and benefits of raising offspring in other delphinids, those with and without post-reproductive lifespan⁸ might help solve this puzzle. There might be other mamas' boys out there.

Killer whales are charismatic top predators that spark our imagination. And they deliver with impressive hunting techniques, diverse cultures and intriguing life history traits. The southern resident killer whale population, which has given the public, and the dedicated scientists studying them, so much in the last 50 years, is on the brink of extinction, largely due to human-made causes such as noise, chemical pollution and prey depletion. Even the most dedicated killer whale mother, with decades of experience, can do little to protect her offspring from such assaults on their environment.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Ecology: How mesopredators run with the big dogs

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Food webs are indispensable maps of community organization, but most are crudely drawn — an inconvenient truth that ecologists must confront. A new DNA metabarcoding study quantifies predator–prey interactions and ecological-network structure with long-overdue precision, supplying insight into how large and small carnivores coexist.

Large carnivores are celebrities, attracting attention wherever they go and rarely being left alone. Scientists watch them closely, too. The classic hypothesis that predators maintain a leafy-green world by controlling herbivore populations¹ inspired decades of research showing that top carnivores can (and often do) influence vegetation, disease dynamics, biogeochemistry and biodiversity². But what about the diverse array of not-so-top carnivores? ‘Mesopredators’ that occupy mid-level spots in food chains, such as mongooses, weasels or foxes, are often overlooked — not just because they are overshadowed by their bigger cousins, but also because their often solitary, nocturnal and elusive lifestyles make them hard to study^{3,4}. Far from being the vermin of popular imagination, or mere bit players in ecosystems, pint-sized predators may play unsung roles as scavengers, seed dispersers and nutrient cyclers^{5,6}. Yet, their ecology, and how they interact and coexist with larger carnivores, remains obscure.

Large and meso-predators interact in complex ways (Figure 1). On the one hand, large carnivores can both eat and compete with smaller ones, dominating

contests for food and space with lethal force; large carnivores frequently kill mesopredators that get in their way^{5,7–9}. On the other hand, large predators can benefit mesopredators by providing free meals in the form of carrion they scavenge from large kills¹⁰. The balance of these positive and negative interactions has rarely been measured but is crucial for understanding how carnivores coexist and the implications of carnivore diversity for ecosystems. Because these interactions revolve

largely around food, knowing who eats what is a must. However, knowledge of food habits is sketchy even for many intensively studied large carnivores, and especially for mesopredators in remote regions. More broadly, the scarcity of detailed dietary data frustrates attempts to forecast ecological dynamics based on the topology of food webs, a major goal in ecology¹¹. A study by Qi Lu, Meng Yao, and colleagues¹² published recently in *Current Biology* tackles these problems, using faecal DNA to reveal



Figure 1. Dangerous game.

Left: a marsh mongoose (*Atilax paludinosus*) enjoys a free meal (carrion of waterbuck, *Kobus ellipsiprymnus*) courtesy of lions in Gorongosa National Park, Mozambique. Right: in almost exactly the same location, a marsh mongoose that met an untimely end, probably also courtesy of lions (photos: Erin M. Phillips).

