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Speculations about southern mergansers (*Mergus* spp.): life history and ecological characteristics inferred from kindred species

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Abstract: Life history and ecological characteristics of extant mergansers (Tribe Mergini) are summarised and used to infer those likely displayed by the extinct merganser from "mainland" New Zealand (*Mergus* sp. indeterm.). I speculate this was a river-dwelling species, plausibly a year-round territorial occupant of mid-lower reaches of rivers, whose subadults and non-breeders may have aggregated seasonally on broad lower reaches, including estuaries. Of extant mergansers, its ecology was probably most similar to that of Brazilian merganser (*Mergus octosetaceus*). Holocene sea-level rise and loss of habitat may have induced changes in social structure of Chatham Island merganser. A plausible life history and ecological template, however speculative, can aid evaluations arising from other sources of evidence e.g. locations of fossils and bone stable isotope chemistry.

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INTRODUCTION

A merganser (*Mergus* sp.) in the New Zealand archipelago is, by any measure, a biogeographic oddity. Mergansers ("sawbills"), a small clade within the "sea ducks" (Tribe Mergini), are of Northern Hemisphere origin, based on Miocene representation (Alvarez & Olsen 1978). Today, they comprise six extant species of *Mergus* (4), *Lophodytes* (1), and *Merganellus* (1), the latter genus alternatively rooted at the split of the *Bucephala* (goldeneye) and merganser clades (Livezey 1995) or having diverged early from the merganser clade (Buckner *et al.* 2018). Their present-day distributions are confined to the boreal and temperate regions of the Euro-Siberian palearctic and to the boreal region of North America with but one exception, the Brazilian merganser (*Mergus octosetaceus*), which is now of remnant distribution on rivers within Brazil's Atlantic forests after having recently disappeared from former enclaves on rivers further south in Paraguay and Argentina (Hughes *et al.* 2006; Lamas & Lins 2020; Campos *et al.* 2023).

Whereas a merganser in South America is evidence of a historic trans-hemispheric crossing, plausibly aided by a land connection and forest-edged riverine pathways, a merganser in the isolated New Zealand region implies an historic, and heroic, trans-hemispheric, trans-oceanic crossing, the when, from where, and by which taxon, continuing to prompt both speculation (e.g. Johnsgard 1960, 1965) and ongoing inquiry (e.g. Livezey 1995; Rawlence *et al.* 2024). Establishing a waif-founded population – as Livezey (1995) colourfully described it – also implies persistent and closely timed arrivals, or an *en masse* founding event, both of which have been rare outcomes in the establishment of New Zealand's land and freshwater avifauna other than from an Australian source (Falla 1953; Trewick & Gibb 2010). With no evidence of an historic merganser presence in Australia, the possibilities of a prolonged oceanic crossing, or of an island-hopping colonising route, most plausibly from a Northern Hemisphere source (Rawlence *et al.* 2024), remain conjectural.

Once established on the New Zealand archipelago, mergansers differentiated. A population, undoubtedly small throughout Holocene times, occupied the subantarctic Auckland Islands, 450 km south of New Zealand and from which it was exterminated, in 1902, following rapacious specimen collecting (Kear & Scarlett 1970; Williams 2012). Another population established on Chatham Island, 800 km east of New Zealand, where, in isolation, it differentiated measurably from those occupying Auckland Islands sufficient to be regarded as a separate taxon (Williams *et al.* 2014).

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It became extinct, most likely from predation by initial Polynesian settlers given that merganser bones have been found in their middens (Sutton & Marshall 1977; Millener 1999). Polynesian settlers, Maori, on the main islands of New Zealand also encountered and ate mergansers. Although merganser bones have been a rare find in Maori midden deposits on North, South and Stewart Islands (Millener 1981; Worthy 1998a,b; Williams *et al.* 2014), predation by Maori, possibly aided by their commensal dog, kuri (*Canis familiaris*), has been proposed as the cause of the merganser's extinction there (Worthy 1999; Tennyson & Martinson 2006). Their former presence was unknown until a mandible was extracted from a midden at Wairau Bar, Marlborough, in 1945 (Kear & Scarlett 1970).

Collectively, the mergansers of the New Zealand region may be referred to as southern mergansers, a name of historic origin – *Harle australe* – applied at the time of initial description (Hombron & Jacquinot 1841). Presently, they are viewed as two species-level taxa: Auckland Island merganser (*M. australis*) and Chatham Island merganser (*M. milleneri*), while the taxonomic status of mergansers on the New Zealand "mainland" (hereafter 'New Zealand merganser') remains unresolved (Checklist Committee 2022), as do the modes of each population's establishment and their relationships with each other. Future taxonomic revision, possibly involving recognition at subspecific level, seems inevitable.

Unaddressed by the current determination to unravel ancestral relationships of southern mergansers is how the birds may have lived, e.g. what habitats were occupied, what foods were consumed, what mating system was displayed? In short, what might have been their life history and ecological characteristics? These questions are explored here.

Drawing initially on Lyell's dictum (Lyell 1864) that (paraphrasing) the past can be explained by reference to contemporary processes, I seek to identify life history and ecological commonalities across all extant sawbills (hereafter 'mergansers') and identify those which can be plausibly imagined as having been displayed by southern mergansers. The implicit assumption is that phylogeny reflects a common ecology, albeit with local adaptations to reflect differing faunistic associations and environmental vicissitudes, and that what is common to all extant mergansers, southern mergansers would have shared.

This approach is a necessary first step to aid future research on, and interpretation of, southern mergansers because they have left a very faint trail. Chatham Island mergansers are known from a fortuitous aggregation of bones from females which nested and became entrapped within a single small cave, from a scattering of 11 wing and leg bones found exposed on the island's sand dunes, and by four bones excavated from middens (Millener 1999; Williams *et al.* 2014). Auckland Island mergansers are known from 27 specimens collected between 1840 and 1902 (Williams 2012), and from four bones found exposed on a sand dune deflation (Tennyson 2020). New Zealand mergansers are represented by bones excavated from seven Maori middens, from three bone aggregations considered to be natural deposits, and four bones found exposed on dune deflations (Worthy & Holdaway 2002; MW *unpubl.*). These locations of bone discovery offer evidence of a former North, South, and Stewart Island distribution, but not of habitat. To date, stable isotope analyses of two bones have

Table 1. Habitats occupied by extant mergansers. Summarised from species accounts in Cramp & Simmonds (1977), Kear (2005), and del Hoyo *et al.* (2020).

Taxon	Breeding	Non-breeding/winter
Goosander	Freshwater lakes, rivers and streams in boreal forested areas, preferring upper basins of rivers and large clear inland lakes. Will use deeper waters and tolerates reaches of fast flow. Seasonal occupancy. Non-territorial.	Predominantly freshwater, on lower latitude lakes, reservoirs and rivers. Sometimes coastal bays and estuaries.
Scaly-sided	On forested-margined, clear, fast-flowing mountain rivers and rapid streams with many shingle spits and islands, in taiga zone; typically, far from human habitation. Seasonal occupancy. Territorial.	Freshwater, most wintering on ice-free lakes, reservoirs, more sluggish rivers and lagoons, but some remain on clear fast-flowing rivers in hilly and mountainous areas, with low disturbance levels (China and Korea) and a small percentage undertakes moult migration to brackish and marine waters (Sea of Japan).
Red-breasted	Sheltered saltwater areas. Riverine occupancy increases with decreasing gradient and prefers slower, smoother river sections. Tundra and boreal forest zones on fresh, brackish, and saltwater wetlands with sheltered bays. Seasonal occupancy. Non-territorial.	Marine. Winters predominantly on secluded bays or estuaries in marine environments where protected areas provide calm seas.
Brazilian	Clear meandering streams with occasional rapids within savannah and subtropical forest, often above waterfalls. Year-round occupancy. Territorial.	Within breeding territories and in areas of unoccupied riverine habitat.
Hooded	Forested lakes, ponds, rivers and streams with clear water (sea-level. to 1180 m asl) across northern-eastern USA and southern Canada. Seasonal occupancy (non-territorial) of central breeding range but year-round in climatically milder eastern range.	Along both coasts, favours forested freshwater wetlands, ponds, brackish estuaries, and tidal creeks, where they often concentrate along the edge of ice.
Smew	Freshwater lakes, pools, slow-flowing rivers and muskegs in taiga zone during breeding season, with preference for lowland oxbow lakes amid forest (including drowned trees), especially within medium-sized valleys, and oligotrophic lakes and rivers with nearby forest in montane or submontane regions. Seasonal occupancy. Non-territorial.	Winters mainly on larger lakes, ice-free rivers, coastal brackish lagoons and estuaries. Uncommonly on open sea and rarely in water more than c. 6 m deep.

provided equivocal indications of diet and feeding realm (Williams *et al.* 2012).

Thus, beyond what this minimal aggregation of remains might be able to convey *per se*, common characteristics of kindred mergansers may provide inferences of key life history and ecological characteristics of southern mergansers. Of particular relevance would be (i) habitat(s) occupied, especially when breeding and whether on rivers, lakes, or in coastal environments; (ii) foods consumed, and the relative importance of fish and invertebrates; (iii) features of breeding biology including whether pair bonds renew annually, whether nesting or territorial philopatry is demonstrated, and whether males contribute parental care; and (iv) any seasonal dispersion including for the wing moult, throughout winter, and of subadults in their pre-breeding years.

KINDRED MERGANSERS

Extant mergansers, in order of descending body mass, are goosander or common merganser (*Mergus merganser*), scaly-sided or Chinese merganser (*M. squamatus*), red-breasted merganser (*M. serrator*), Brazilian merganser, hooded merganser (*Lophodytes cucullatus*), and smew (*Mergellus albellus*). Their distributions, and details of their sexual dimorphism in plumage and body sizes, are well documented (Kear 2005; del Hoyo *et al.* 2020), and attest to southern mergansers being the most geographically isolated and, at an estimated 550-760g (Williams 2012), the smallest *Mergus,* and approaching the conspicuously smaller hooded merganser and smew in body size.

Habitats

The five Northern Hemisphere mergansers are characterised by their seasonal occupancy of different habitats, whereas the Brazilian merganser is a year-round river resident (Table 1). Freshwaters are the primary environment for all. Breeding habitat is typically forest-edged watercourses or secluded lake shores throughout the boreal region, some extending into sub-arctic waterways. The red-breasted merganser is the only species known sometimes to breed in or adjacent to saline water and has been recorded nesting amongst colonial-nesting seabirds on near-shore islands (Craik *et al.* 2020).

Ice-free freshwaters comprise the main winter habitats of all northern mergansers, requiring some extensive seasonal migrations. All except hooded merganser have been recorded sometimes aggregated in protected coastal or estuarine locations for their annual wing moult and persisting there during hard winters (del Hoyo *et al.* 2020).

Foods and feeding

All mergansers consume both fish and aquatic invertebrates in all of their habitats (Table 2). Feeding on fish commonly involves scanning from the water surface before diving, the prey being consumed at the surface rather than underwater. Fossicking for invertebrates occurs from the surface in shallow water, or by prolonged dives in deeper water. The relative importance of these two food categories has not been well established except that all feeding studies report a mixed diet but, depending on sampling time or place, may be dominated by one food type. For ducklings of all species, sessile and motile invertebrate prey are the primary foods until they are about half-grown. Uniquely, Brazilian mergansers will feed fish to their ducklings. Co-operative feeding, which assists the capture of fast-moving schooling fish, has been reported for all northern mergansers when aggregated as flocks.

Life history and breeding characteristics

All extant mergansers first attempt to breed in their second year, or later (Table 3). Their delayed maturity has the likely correlate of extended longevity, although data to support this assumption are sparse for all species. Seasonal monogamy is common to all northern mergansers, with pairings being established during spring migration or on the breeding grounds. Males of these species abandon their mates from midway through the incubation period (30–34 days), and well before hatching. Females alone provide parental care. Nesting is mostly in tree holes or root boles, and some nest sites are occupied in consecutive years. Amalgamation of broods occurs amongst neighbouring river-dwelling families but has not been reported in the more spatially dispersed hooded merganser and smew.

Female breeding area fidelity is well attested for red-breasted mergansers (Craik *et al.* 2020) and is implied by records of some goosander (Eriksson & Niittylä 1985),

Table 2. Foods of extant mergansers. Summarised from species accounts in Cramp & Simmonds (1977), Kear (2005), and del Hoyo *et al.* (2020).

Taxon	Saline/Marine		Freshwater	
	Invertebrates	**Fish**	**Invertebrates**	**Fish**
Goosander	Large benthic prey taken.	Predominantly piscivorous. Co-operative feeding.	Larger benthic prey taken but seemingly as a supplement.	Predominantly piscivorous, no obvious prey selection although salmonids feature in many analyses.
Scaly-sided	Large benthic prey probably taken.	Predominantly piscivorous. Co-operative feeding.	Diurnal feeder, taking mainly small fish and aquatic invertebrates.	
Red-breasted	Large benthic prey, including crustacea and worms.	Predominantly piscivorous. Co-operative feeding.	Unselective, gleans caddis, small crustacea, worms.	Predominantly piscivorous.
Brazilian	Marine habitats not occupied		Extensively	Extensively
Hooded	Yes	Yes	Insects, crustacea (particularly crayfish),. more so than other mergansers.	Primarily fish and crustaceans.
Smew	Annelids, crustacea, rarely small bivalves.	Any small fish. Flock feeding in winter across sandy sea floors.	Most aquatic invertebrates (water beetles, dragonflies, caddis larvae).	Both pelagic and bottom-dwelling species.

Table 3. Breeding characteristics of mergansers. Summarised from species accounts in Cramp & Simmonds (1977), Kear (2005), and del Hoyo *et al.* (2020). n.d. = no data.

Taxon	Year of first breeding	Mate fidelity	Clutch size	Incubation (days)	Nest site	Parental care	Brood amalgamation
Goosander	2nd	Seasonal monogamy	8–11	30–32	Tree and other cavities	Female only	Common
Scaly-sided	2-3	Seasonal monogamy	10–11	31–35	Tree cavities	Female only	Common
Red-breasted	2nd	Seasonal monogamy	8–10	31–32	Concealed ground sites	Female only	Common
Brazilian	n.d.	Long-term monogamy	5–8	c.33	Tree and ground cavities	Bi-parental	Not reported
Hooded	2nd	Seasonal monogamy	9–11	29–33	Tree cavities	Female only	Not reported. Frequent nest parasitism
Smew	2nd?	Seasonal monogamy	7–9	26–28	Tree cavities	Female only	Not reported. Nest parasitism referenced

hooded merganser (Duggar *et al.* 2020), and scaly-sided merganser (Zhaio *et al.* 1995) females reusing nest cavities, or nesting again nearby.

Brazilian mergansers are distinguished from their northern counterparts by occupying and defending their breeding territories throughout the year. This behaviour is accompanied by enduring multi-year pair bonds, shared parental care of offspring, and prolonged retention of fledglings within their natal areas. They are also distinguished by their extensive feeding ranges and low-density occupation of their riverine habitat.

Seasonal dispersion

Adult males and females of northern mergansers have different patterns of seasonal dispersion. After abandoning females on the breeding grounds, males migrate to (mostly) sheltered coastal locations to undergo their annual wing moult, before dispersing again ahead of winter ice formation. Females of most species also assemble in moult aggregations, but mostly at freshwater sites closer to breeding areas. From there they disperse back to breeding areas by following the spring ice retreat (species accounts in del Hoyo *et al.* 2020).

Delayed maturity results in subadults (young of the previous year) being present in loose aggregations at moulting and breeding sites. Small flocks sometimes assemble on river sand bars from where they move at length up and down rivers to become familiar with occupied and potential breeding habitats.

Commonalities and differences

Multiple characteristics differentiate the Brazilian merganser from the others. Northern Hemisphere mergansers have ecologies and life histories shaped by their seasonal occupation of breeding habitat on woodland-margined freshwaters (including river segments comprising pool/riffle systems with swift-flowing or turbulent water), commencing from when the spring thaw is advanced enough to offer ice-free waters in which to feed, and by the subsequent seasonal necessity to seek ice-free winter refuges. Seasonal monogamy and female-only parental care characterise this life history, as do long migratory flights to communal moulting and feeding sites, some of which include saline environments.

By contrast, Brazilian mergansers are year-round occupants of their present-day tropical rain forest riverine habitat, and long-term breeding partnerships are indicated. Even so, many of their life history and ecological characteristics e.g. delayed maturity, tree hole nesting sites, swift-flowing riverine breeding habitat, and food diversity, mirror those of northern mergansers, and are indicative of the transfer of basic life history traits into a warmer, wetter, and snowless environment. This being so, the Brazilian merganser may model how southern mergansers, in their temperate environments, may have lived.

There is an important proviso, however. Presently, Brazilian mergansers have a remnant distribution. Descriptions of all persisting population isolates as occupying habitat of ”rapid, torrential streams and fast-flowing rivers usually fringed by dense tropical forest, typically selecting rivers > 1 m deep and > 3 m wide, though after rains, when main rivers may become turbid with sediment, apparently uses shallow streams just *c.* 50 cm deep and 2–4 m wide” (Carboneras *et al.* 2018), may not necessarily reflect optimal habitat requirements, nor that of former habitats now alienated (Gray & Craig 1991; Lomolino 2023). Similarly, interpretations of breeding density e.g. “territory size (of multiple kms length) believed to be related to number of rapids, edge waters, water speed, fish abundance and conservation of riparian vegetation” (Carboneras *et al.* 2018), may also reflect the small sizes of present populations. These disjunct remnant populations have not yielded evidence of inter-catchment dispersal or settlement, nor of dispersal beyond forest-fringed waterways. Review literature makes no reference to Brazilian mergansers inhabiting lakes or impoundments. Some Brazilian rivers on which they occur have been modified by small hydro dam construction and water impoundments. Mergansers are absent from these lentic environments (Bovo *et al.* 2021).

Nonetheless, the critical conservation status of the Brazilian merganser has fostered multiple studies of its life history and reproductive characteristics, including those of Bruno *et al.* (2010), Vilaca *et al.* (2012), and Ribiero *et al.* (2018), and all have highlighted the merganser’s multi-year site occupancy and territoriality, enduring mating relationships, a diminished mean and range in clutch size relative to northern mergansers, bi-parental brood care, and the prolonged presence of young within their natal range, hinting at natal philopatry and confirming delayed onset of breeding.

SPECULATIONS ABOUT THE NEW ZEALAND MERGANSER

The following speculations about the New Zealand merganser are based on the preceding summaries of contemporary merganser life histories and ecological characteristics, and the contrasts between those of the Brazilian and northern mergansers.

Habitat

New Zealand mergansers occupied forested-edged rivers as breeding habitat.

All extant mergansers occupy forest-edged riverine habitat that includes pool/riffle systems thus indicating an ability to capture or glean prey in swift-flowing or turbulent water. If such areas of New Zealand rivers had a year-round abundance of small fish (for it seems unlikely that southern mergansers could have been sustained by a diet solely of freshwater invertebrates), mergansers might have occupied mid-gradient (10–25 m/km) segments of rivers well inland, perhaps even occupying some waters in which whio/blue duck (*Hymenolaimus malacorhynchos*) might also have occurred. Like other *Mergus* species, they were likely dispersed at low density (multiple kms/pair).

Mating system

New Zealand mergansers maintained year-round and exclusive occupancy of their breeding habitats and maintained pair associations year-round. Bi-parental brood care, or at least male brood attendance, would have occurred and both adults would have undertaken their annual wing moult within their breeding range.

This speculation directly reflects the Brazilian merganser's mating system and assumes the breeding habitat provided sufficient food resources to support autumn-winter occupancy (see below). It also reflects characteristics common to most other riverine waterfowl (Williams & McKinney 1996), especially those occupying habitat hazardous to ducklings. In these respects, the mating system of the New Zealand merganser may have been similar to that of whio/blue duck, New Zealand's other riverine waterfowl (Williams 2013).

Life history

Breeding was delayed until at least the second year, and subadults comprised an itinerant component of the population.

Delayed maturity is a characteristic of all extant merganser species. In common with many other waterfowl species with delayed maturity (Oring & Sayler 1992), subadults would have traversed breeding habitat and interacted with resident breeders. They were also likely to have co-assembled in non-breeding habitat, there to feed and undergoing their wing moults collectively. These habitats would have included river deltas and their estuarine zones, especially during times of fish migrations.

Fish resource

Freshwater fishes in rivers of pre-human New Zealand were sufficiently abundant, year-round, to support an avian piscivore.

Of the 38 fishes native to New Zealand, about half spend part of their life histories, as juveniles, in the sea (McDowall 1990), and most reach the rivers in large spring-time migrations. Thereafter, upstream movements disperse species to a variety of watercourses, large, small and occluded, and those species with climbing abilities circumvent obstacles to reach headwaters. Likely biomass in rivers prior to human settlement can only be surmised; however, some species were so profoundly abundant, especially when migrating, that they provided a plentiful and reliable seasonal food resource for Maori (McDowall 2011; Anderson 2025), especially eels (Family Anguillidae), grayling/upokororo (*Prototroctes oxyrhynchus*: Retropinnidae), and multiple species of "whitebaits" (Family Galaxiidae). Conspicuous amongst the latter were inanga (*Galaxias maculatus*), koaro (*G. brevipinnis*), and kokopu (*G. argenteus*). Early European accounts (as interpreted by McDowall 2011) indicate an abundant year-round presence of eels, grayling, and koaro in segments of rivers 'modest distances inland', while koura/freshwater crayfish (*Paranephrops planifrons, P. zealandicus*) were probably then common and abundant.

POSSIBLE INDEPENDENT ADAPTATIONS OF CHATHAM ISLAND AND AUCKLAND ISLAND MERGANSERS

Whereas northern mergansers probably responded to the successive Pleistocene era advances and retreats of ice sheets across their continental ranges by moving south or north with them, southern mergansers faced significant expansion or diminution of landscape in response to associated sea level changes. For example, the dramatic rise of sea level since the last glacial maximum (Clarke *et al.* 2009) drowned extensive lowland riverine habitat within the ranges of all three southern mergansers. Using the present-day 120 m seafloor contour as a proxy for likely shoreline at the last glacial maximum (21-18,000 years before present), land areas of Chatham and Auckland Islands have each been reduced by *c.* 88% and New Zealand itself by *c.* 35% (D. Strogen, *pers. comm.*). The New Zealand mainland was also cleaved into its present three main islands.

At Chatham Island, such extensive loss of most riverine and estuarine habitat probably greatly diminished the merganser population. Sea-level stabilisation, from about 6,000 BP, allowed the formation of the shallow but extensive (160 km^2) Te Whanga Lagoon, thereby providing an essential, possibly primary, estuarine refuge for the mergansers. Whether in response, or already a prior adaptation, Chatham Island mergansers displayed an obvious tolerance for feeding in marine and estuarine waters. Their skulls bear prominent supra-orbital salt gland impressions (Williams *et al.* 2014: Fig 3), visibly larger and more conspicuous than on the skulls of northern mergansers (viewed at https://skullsite.com). Bone stable isotope measurements from three mergansers which nested alongside the lagoon confirmed a saline feeding environment and a diet probably dominated by piscivorous fish (Williams *et al.* 2012).

Dependence on foods from expansive and featureless marine/estuarine environments would probably have required a social structure different from that shown by all extant river-breeding mergansers, or that speculated for New Zealand mergansers. Exclusive resource acquisition and defence of a fixed area, even just seasonally, would likely have proven unobtainable, just as it is for many waterfowl whose feeding environments are widely distributed, including as multiple small patches e.g. many *Anas* ducks (Baldassare & Bolen 2006). Chatham Island mergansers might have made significant behavioural changes as part of their adaptation to a rapidly changing and shrinking Holocene feeding environment.

At Auckland Island, its landscape has long been dominated by steep and truncated glaciated valleys descending its eastern flank. Holocene sea-level rise (implied by the 120 m seafloor contour) inundated formerly extensive north-eastern lowland and associated meandering waterways. No coastal waters protected from the endless westerly or southerly tempests remained, except at the very heads of most eastern valleys, or along short sections of Carnley Harbour. During its brief period of human encounter (1840–1902), the Auckland Island merganser was a rarity, observed only within some short, steep valley streams and their immediately adjacent coastal fringes (Williams 2012). Although stable isotope measurements of its bones, claws and feathers indicate both freshwater and marine-sourced foods, salt gland impressions are barely discernible on its skull (Williams *et al.* 2012). By having occupied discrete and delineable habitat, Auckland Island mergansers may have evinced a social structure and mating system akin to those suggested for the New Zealand merganser, albeit in very small numbers. The only two broods of ducklings observed were each accompanied by two adults (Williams 2012).

CONCLUSIONS

Whereas, at the time of first human settlement, Chatham Island's and Auckland Island's merganser populations were small and largely restricted to habitats and foods in estuarine and saline waters, I speculate that New Zealand's merganser was a riverine species. In common with all extant *Mergus*, its breeding pairs were probably dispersed at low density along low to mid gradient reaches. Subadults and non-breeders, in addition to traversing breeding areas, would likely have aggregated, seasonally or persistently, on more extensive lowland reaches and any associated estuary. Of extant mergansers, the life history and ecological characteristics of Brazilian merganser, remnant populations in small refugia though this species now comprises, can provide a useful model for interpretating the ecology of New Zealand mergansers garnered from other sources, such as middens and natural deposits of merganser bones, and evaluations of bone protein isotope chemistry.

New Zealand's other endemic river-dwelling waterfowl, whio/blue duck, is particularly rare as a fossil, and although found in cave deposits, arising from its habit of fossicking seepages and trickles beyond watercourses (Worthy & Holdaway 2002), it has not yet been retrieved from midden deposits. Nor was it recovered from the only two lacustrine deposits reported (Pyramid Valley, Holdaway & Worthy 1997; Lake Poukawa, Worthy 2004).

Although merganser bones were found in the Lake Poukawa deposit, perhaps a tantalising hint of another habitat exploited, it has been the rare recovery of merganser bones in estuarine-edge Maori midden deposits (Kear & Scarlett 1970, Worthy 1998a; Worthy & Holdaway 2002) that has prompted a prevailing interpretation of the New Zealand merganser being a coastal and marine inhabitant (e.g. Heather & Robertson 1996; Worthy1998a,b; Tennyson & Martinson 2006). Locations of Maori midden deposits reflect human choice of occupation site. Whether foods were gathered locally or more widely is difficult to determine. While avian species composition in middens might indicate the immediate environments from which food was collected, relative species abundance is more problematic to interpret (Scofield *et al.* 2003; Worthy 1999). For any interpretation, the challenge is to separate human agency from natural phenomena, a challenge perhaps aided by the question 'what aspect of this merganser life history or ecology might have allowed bones to accumulate here?' This is especially relevant to sites near middens yet deemed to be natural deposits and from which bones of multiple merganser individuals have been extracted e.g. Marfells Beach, Native Island, and Lake Poukawa (Worthy 1998a,b, 2004). Stable isotope analyses of these bones, in conjunction with secure understanding of their provenance, can test the speculative inclusion of this merganser as a member of New Zealand's endemic freshwater avifauna.

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