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Minor differentiation of foraging niche may have a major impact on the incidence of avian botulism in shorebirds

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Abstract

Avian botulism is a fatal disease of birds caused by ingestion of neurotoxins produced by *Clostridium botulinum* type C and is now recognized as the most common cause of death in waterbirds worldwide. Although tens of species have been reported to suffer from avian botulism, it remains unknown which ecological factors primarily determine inter-specific variation in the incidence of this disease. We hypothesized that an exposure of birds to botulin may largely depend on their foraging niche, as the toxin is available mostly at the sediment surface, especially during the carcass-maggot stage of botulism epizootics. To test this hypothesis we used capture-recapture methods to estimate mortality of two shorebird species differing in bill morphology and foraging niche, wood sandpiper *Tringa glareola* (short bill, surface-feeding) and common snipe *Gallinago gallinago* (long bill, deep probing), during a major avian type C botulism outbreak in central Poland. All the reported cases of shorebird mortality were attributed to botulism and we found large differences in daily survival rates of both species (0.87 and 0.99 in wood sandpipers and common snipe, respectively). Even assuming much shorter stopover duration of wood sandpipers, survival rate over the entire stopover period was estimated at 0.57 in the wood sandpiper and at 0.90 in the common snipe. To our knowledge, this is the first non-circumstantial evidence that relatively minor differentiation of foraging niche may have a major impact on the incidence of avian botulism in birds. Our data might also suggest that, on the evolutionary time scale, avian type C botulism may constitute a strong selective pressure acting on foraging niches of shorebirds, and possibly other waterbirds.

Zusammenfassung

Botulismus ist bei Vögeln eine tödliche Krankheit, die durch die Aufnahme von Neurotoxinen, die von *Clostridium botulinum* Typ C produziert werden, hervorgerufen wird und mittlerweile als die weltweit häufigste Todesursache bei Wasservögeln erkannt worden ist. Wenn auch bei Dutzenden von Vogelarten Botulismus gefunden wurde, ist unbekannt, welche ökologischen Faktoren hauptsächlich die interspezifischen Unterschiede in den Fallzahlen bestimmen. Wir nahmen an, dass der Kontakt zum Butulinumtoxin weitgehend von der Nahrungsnische abhängen sollte, weil das Toxin meist auf der Oberfläche des Sediments vorhanden ist, insbesondere während der Maden-Kadaver-Phase von Botulismus-Seuchen. Um diese Hypothese zu testen, nutzten wir während eines größeren Botulismusausbruchs in Mittelpolen Fang-Wiederfang Methoden zur Bestimmung der Mortalität von zwei Limikolenarten, die sich hinsichtlich Schnabellänge und Nahrungsnische unterscheiden: Bruchwasserläufer *Tringa glareola* (kurzer Schnabel, Nahrungssuche auf dem Sediment) und Bekassine *Gallinago gallinago* (langer Schnabel, stochert tief im Untergrund). Alle registrierten Sterbefälle der Limikolen wurden auf Botulismus zurückgeführt, und wir fanden große Unterschiede für die täglichen Sterberaten von Bruchwasserläufer (0,87) und Bekassine (0,99). Selbst wenn man eine deutlich kürzere Aufenthaltsdauer für den Bruchwasserläufer annimmt, war seine Überlebensrate für die gesamte Aufenthaltsdauer viel geringer

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(0,57) als bei der Bekassine (0,90). Nach unserer Kenntnis ist dies der erste direkte Hinweis darauf, dass ein verhältnismäßig kleiner Unterschied in der Nahrungsnische größeren Einfluss auf die Häufigkeit von Botulismusfällen bei Vögeln haben könnte. Unsere Ergebnisse könnten auch nahelegen, dass in evolutionären Zeiträumen Botulismus Typ C einen starken Selektionsdruck auf die Nahrungsnischen von Watvögeln und möglicherweise anderen Wasservögeln ausübt.

Keywords: Capture-recapture; *Clostridium botulinum*; Foraging niche; Shorebirds; Survival rate; Type C botulism

Introduction

Avian botulism is a paralytic and often fatal disease of birds caused by ingestion of neurotoxins that are produced by *Clostridium botulinum* type C (Rocke and Bollinger 2007). Sporadic avian mortality has also been caused by type E toxin, although it has been reported almost exclusively for fish-eating waterfowl (Brand, Schmitt, Duncan, & Cooley 1988; Hannett, Stone, Davis, & Wroblewski 2011). Under aerobic and other adverse conditions, *C. botulinum* forms dormant spores, which are harmless until they germinate into vegetative cells and begin multiplying. After germination, bacterial cells may start to produce neurotoxins which are encoded by specific bacteriophages that infect and replicate specifically within *Clostridium* bacteria (Eklund, Poysky, Reed, & Smith 1971). Optimal environmental conditions that promote germination of botulinum spores are relatively poorly recognized, but botulism outbreaks usually develop in shallow waters that are rich in decaying organic matter (Rocke and Samuel 1999).

In order for a botulism outbreak to occur the toxin must become available for birds. In the early stages of epizootics the toxin is presumably transferred from the substrate to the birds through zooplankton and benthic epifauna. Invertebrates that feed on decaying matter remain unaffected by the toxin and may act as toxin reservoirs (Duncan and Jensen 1976; Rocke and Bollinger 2007). An alternative route to a massive botulism outbreak is through toxicoinfection, resulting from ingestion of *C. botulinum* spores, followed by multiplication of bacteria within the gastrointestinal tract, with subsequent toxigenesis and absorption of toxins (Critchley 1991; Trampel, Smith, & Rocke 2005). Thus, the incidence and numbers of *C. botulinum* spores and vegetative cells, as well as the concentration of botulinum neurotoxin in the environment could contribute significantly to the onset of a large outbreak. As soon as the first botulism-related casualties occur, an outbreak often becomes self-perpetuating, as foraging waterbirds tend to accidentally ingest toxic fly larvae that feed on the carcasses of infected birds. This, so called, carcass-maggot cycle rapidly accelerates the spread of the disease, causing massive avian botulism outbreaks (Espelund and Klaveness 2014). In fact, outbreaks with losses of up to 50,000 birds are relatively common and botulism epizootics with more than a million deaths have been reported (Rocke and Bollinger 2007). In consequence, avian botulism has been recognized as the most common cause of death in waterbirds worldwide.

Most shorebirds (Charadrii) typically use shallow water and mudflat habitats to replenish fuel reserves during migration and, thus, are potentially highly exposed to avian botulism. However, this group of birds shows extraordinary divergence of micro-habitat use and foraging niche, mostly attributable to high inter-specific variation in bill morphology (Nebel, Jackson, & Elner 2005). One of the primary determinants of foraging behavior in shorebirds is bill length, as species/individuals with shorter bills are expected to peck epifaunal prey or probe near the sediment surface, while species/individuals with longer bills probe deeper into the sediments and feed mainly on infaunal invertebrates. We hypothesized that such differentiation of foraging niche may have an impact on the incidence of avian botulism, as botulinum toxins are available mostly at the sediment surface, especially during the carcass-maggot stage of botulism epizootics. To test this hypothesis we used capture-recapture methods to estimate survival rate of two shorebird species differing in bill morphology, wood sandpiper *Tringa glareola* and common snipe *Gallinago gallinago*, during a major avian type C botulism outbreak. Wood sandpiper has a relatively short bill (interquartile range: 27.0–28.8 mm, Fig. 1) and it

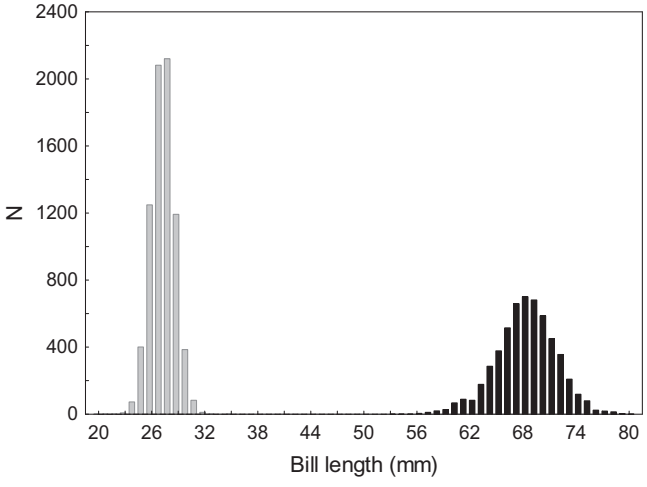

Fig. 1. Divergence in bill length among wood sandpiper (grey bars, $n = 7609$ individuals) and common snipe (black bars, $n = 5569$ individuals). Data collected during autumn migration period between 1989 and 2013 at Jeziorsko reservoir, central Poland.