SONG TYPE PREFERENCES DURING THE DAWN CHORUS IN MALE ADELAIDE'S WARBLERS (*SETOPHAGA ADELAIDAE*)

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DEDICATION

I dedicate this thesis to the God of my journey, who has been with me every step of the way. To El-Roi, the God that sees me - no detail of my life escapes his watchful eyes. Yet, He continues to show me mercy daily and make me a spectacle of his glory.

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ABSTRACT

Songbirds sing a repertoire of song types, some of which are shared with neighbours. Songbirds prefer certain song types, but the reasons for these preferences are not well understood. I analyzed 11,800 dawn chorus songs from 14 male Adelaide's warblers (*Setophaga adelaidae*) to determine if males exhibit preference for specific song types and if these preferences are consistent across recording days. Each male had an average repertoire of 21.27 ± 3.62 song types. All males had song preferences, with the most preferred song type accounting for 17% of their song output. Song type preferences were consistent across days. I then omitted recordings that were not amenable to acoustic analysis, resulting in a reduced dataset (n = 9395), which I used to test whether males prefer (1) widely shared (locally prevalent) song types, (2) song types with superior transmission properties, or (3) song types with high or low vocal performance. I found strong evidence that males preferred widely shared songs, but the evidence for the second hypothesis was mixed. Males preferred song types with low frequency and low percent sound, supporting two predictions of the efficient sound transmission hypothesis. However, they did not prefer songs with high amplitude or high vocal deviation, negating the other two predictions of that hypothesis. Males preferred song types with low percent sound, as expected by the third hypothesis if they prefer songs with low performance requirement, but amplitude and vocal deviation had little effect on preference. This study supports the Social Dynamics Hypothesis, which states that social factors influence Adelaide's warblers' song type preference during the dawn chorus. Song sharing within the local communication networks influences male song preferences, although acoustic transmission properties and vocal performance may play a role as well.

CONTRIBUTIONS OF AUTHORS

I was the lead author on all sections except field methods (Chapter 2.2). My other contributions to this thesis include blind song type scoring, data management, analysis, and visualization. Data collection and scoring for this study were conducted by former and current lab members, including David M. Logue, Kenneth X. Rodriguez-Rivera, Karla Vílchez-Castaño, Pablo Sosa-Negrón, Heath Petkau, Samantha Huang, and Juleyska Vazquez-Cardona. Rylie Mooney and David M. Logue conducted the acoustic analysis. David M. Logue collaborated with me on data management and analysis, led the writing of the field methods section, and edited all chapters. Tyler R. Bonnell advised on the Bayesian models.

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LIST OF ABBREVIATIONS

Bird ID	Bird identification
ISTs	Within-individual male song types
ST(s)	Song Type(s)
USTs	Universal song types

CHAPTER 1: FUNCTION AND MECHANISM OF SIGNAL PREFERENCE IN SONGBIRDS

1.1 Signal repertoire and preferences

Imagine a world where every gesture, sound, and scent carry a message. This is the reality for animals, who rely on signals to communicate. A signal is a trait or behaviour that evolved because of its influence on signal receivers' behaviour (Bradbury & Vehrencamp, 2011; Smith & Harper, 2003). Animals use many different signals to influence one another's behaviour. Signals may indicate the presence of a potential mate or rival, the threat of a predator or hazard, the nutritional needs of offspring, the identity of a nest or colony mate, and more (Wiley, 2013). A signal repertoire is a set of communicative signals used by an individual or species. To understand how animal communication evolves and functions, it is essential to consider not just the variety and function of signals but also the preferences that shape how signals from an animal's repertoire are produced and perceived.

Signal preference is the tendency to favour certain types of signals over others. Receiver preference is the inclination of the receiver to perceive and respond to certain types of signals. This preference is often based on what the signal receiver finds more attractive, informative, or beneficial. For example, a female bird might prefer certain songs that indicate a healthy potential mate (Catchpole & Slater, 2003). Sender preference, on the other hand, is the inclination of the sender (the individual producing the signal) to choose a specific signal type from its repertoire. In this study, I focus on senders' preferences in songbirds. Songbirds develop preferences for certain signals due to social learning, sexual selection, and adaptations to their habitat.

1.1.1 Social learning can cause signal preference

Early life experiences and social learning processes have a significant impact on the development of signal preferences (Beecher & Burt, 2004). Senders often learn to produce specific signals through direct interactions with their habitat and conspecifics. Songbirds, for example, learn their songs by listening to and imitating adult conspecifics during a sensitive period in their development (Marler, 1970). This learned behaviour ensures that their signals are appropriate for their social and ecological context.

Social learning enhances signal preference development. Animals, particularly those living in social groups, often learn preferences by observing and mimicking others (Galef & Giraldeau, 2001). This process helps them learn what is beneficial and preferred within their group.

1.1.2 Sexual selection-based causes of signal preference

Sexual selection and mate choice also play a role in the development of signal preferences. Receivers often prefer signals that indicate high quality from potential mates (Andersson, 1994; Ryan, 1998). Receivers' preferences drive the evolution of senders' preferences, as selection causes senders to produce signals that align with what receivers find appealing. For example, in many bird species, females may prefer males with more elaborate songs or brighter plumage. These traits often serve as indicators of good health, genetic fitness, and overall viability, making them attractive to potential mates (Searcy & Nowicki, 2005). As a result, males with these preferred traits are more likely to reproduce, leading to the proliferation of these characteristics in subsequent generations, if sender preferences are heritable. West and King (1988), in their study on cowbirds (*Molothrus ater*), verified that males observe female reactions that their signals elicited. Male cowbirds adjust their songs based on female feedback, by singing more song elements that elicit strong responses in females. The receivers' preference shapes the senders' preference.

Competition can also influence signal preferences. In many species, signals that are effective in deterring rivals or establishing dominance are particularly favoured. For instance, in species where competition for territory or mates is fierce, individuals may develop a preference for signals that are more conspicuous, such as louder calls, brighter colours, or more aggressive displays (Smith-Vidaurre et al., 2020). These signals serve to intimidate rivals and assert dominance, thereby improving the signaler's chances of winning conflicts and securing resources or mates. Over time, this competitive pressure can lead to the selection of increasingly bold or aggressive signals within the population.

1.1.3 Habitat-based causes of signal preference

The habitat in which an animal lives can influence the evolution of signal preferences. Habitat-specific factors determine the efficacy of different signals, thereby shaping preferences. Visual signals, for instance, may be more effective in open habitats where they can be easily seen, while acoustic signals may be more advantageous in dense forests where visibility is limited (Endler, 1993). The efficacy of a signal in a given habitat plays a crucial role in shaping communication strategies and preference development in different species. Both selection and learning may influence senders to prefer signals that are easily transmitted and received in a particular environment. The acoustic properties of the habitat or the visibility of certain colours may determine which kinds of signals are preferred. For example, in densely vegetated areas, animals tend to favour low frequency acoustic signals because they travel farther than high frequency signals. In contrast, in open habitats where visual signals are more effective, bright and contrasting colours may be preferred for communication. The selection of signals also depends on the specific ecological pressures faced by the species. For instance, in environments with high levels of background noise, animals may evolve signals that are more easily distinguished from the surrounding soundscape. Also, the presence of predators may influence the evolution of signals that can effectively convey information about potential threats (Bradbury & Vehrencamp, 2011).

1.2 Vocal signals in birds

Birds produce vocal sounds from their respiratory systems, like humans and other mammals. Unlike mammals, however, birds use a special vocal organ called the syrinx at the base of the trachea to make vocal sounds. Birds make a variety of sounds with the syrinx by changing the air pressure and controlling their muscles (Catchpole, 1986). Birdsong complexity and diversity stem from their vocal tract and the intricate control birds have over it.

Birds produce two kinds of vocal signals: calls and songs. Calls are brief sounds, typically produced by both sexes. Most calls do not require learning from adults. Types of calls include distress calls, flight calls, alarm calls, feeding calls, and flock calls (Gill, 1995). For example, young birds use feeding calls to get their parents to feed them, while alarm calls are used to let other birds know when there is danger.

Songs are longer, louder, and more complex than calls. Birds in the order Passeriformes are divided into two suborders: the oscines (or songbirds) and the suboscines. Oscines, which include species like sparrows, robins, and warblers, are noted for their advanced vocal learning abilities and complex song production. In contrast, suboscines, which include birds like flycatchers, ovenbirds, and antbirds, have simpler songs that develop normally without learning from a model (Baptista & Kroodsma, 2001). Both male and female birds sing in many tropical and southern hemisphere species. However, females do not sing in most north temperate species. Among females that do sing in these regions, female songs are generally less elaborate than those of their male counterparts (Odom et al., 2014; Riebel et al., 2019).

Bird songs serve two major functions: mate attraction and resource defence (Catchpole & Slater, 2003; Gil & Llusia, 2020; Kroodsma & Byers, 1991). As such, selection has shaped songs to make them attractive to mates and repellent to rivals. Because singers must show off, songs often evolve to be more costly to sing, making them harder to cheat on as signals of quality (Marler & Slabbekoorn, 2004). In addition to the singer's quality, songs can also communicate species identity, individual identity, natal area, population residency, and other information (Kroodsma & Byers, 1991).

Bird songs evolved because they affect the behaviour of the birds that hear them. Listening birds use variations in song traits to make important decisions that affect their survival and reproduction. Receivers' preferences shape the song traits that (senders) develop and prefer to use, as described above in the brown-headed cowbird example. Whether it is based on learning or selection, this kind of feedback loop leads to the optimization of song types that affect receivers' behaviour.

1.3 Song type repertoire and song learning in songbirds

Individuals of many species of songbirds sing a repertoire of distinct songs, called "song types." Each song type is characterized by unique acoustic structures (Brenowitz et al., 1997). Some species have extensive repertoires, while others have only one or a few song types. Because of vocal learning, birds often share some of their song types with their neighbours. Factors such as habitat, social organization, and mating strategies have an impact on the variation in song repertoire size and complexity among various species of songbirds (Molles & Vehrencamp, 1999).

To grasp how vocal interactions work, it is important to know how songs are learned and how they function. Young birds develop song type repertoires because of their social and vocal interactions with adult conspecifics. They learn songs by listening to adults in their neighbourhood. Social interactions of young birds with older birds in the population have an impact on the songbirds' ability to learn songs (Beecher et al., 1994). While laboratory studies revealed that social factors are key in song learning, little is known about how birds choose the songs they learn under natural conditions.

In some species, birds learn more songs than they sing in adulthood. This phenomenon is known as "overproduction and selective attrition." Selective attrition occurs when birds reject memorized heterospecific song elements (Peters & Nowicki, 2017). Overproduction and attrition may enhance a male's ability to selectively produce songs that are more effective at mate attraction. An example of this is the male brown-headed cowbird (*Molothrus ater*), who responds to visual signals from females, such as wing movements and beak gapes, during their first breeding season and retains song materials that elicit positive female response (King et al., 2005; Peters & Nowicki, 2017).

Countersinging, in which neighbouring territory owners sing back-and-forth, may also influence the evolution of male repertoires (Logue, 2021). Groups of territorial birds that interact vocally can form a communication network, with each bird sending and receiving signals. Song type matching and its variations are common during countersinging. Typical song type matching occurs when one bird responds to another's song by singing the same type of song. A bird can engage in "repertoire matching" by singing a song type that is not the same as its counterpart's most recent song type but is still within the repertoire of the counterpart.

Countersinging interactions like song type matching and repertoire matching suggest that song type preferences may be shaped not only by individual performance constraints but also by social dynamics, where matching or deviating from a counterpart's song can influence social relationships or territorial disputes (Catchpole & Slater, 2003; Searcy & Beecher, 2009). Moreover, song type prevalence, the number of males that share a song type within a population, may also play a role in shaping male preferences. Prevalent songs, being more commonly heard, could provide a shared "acoustic currency" that facilitates communication, while less prevalent songs might offer opportunities for individual distinction or innovation during countersinging interactions (Catchpole & Slater, 2003; Logue, 2021).

Social factors play a major role in song learning, and it is likely that they also influence the young bird's song type preference. Two social factors relevant to song learning in birds are direct interaction and social eavesdropping. Direct interaction occurs when young birds learn songs directly from song tutors through social contact with their neighbours, while social eavesdropping occurs when birds learn by eavesdropping on interacting singers (Beecher & Akçay, 2021). Songbirds also learn songs from unrelated individuals and engage in complex social interactions through vocalizations. Young birds that eavesdrop on social interactions may also learn the rules that govern countersinging (Logue, 2021). Now that we understand the foundation of social interactions that influence vocal development in songbirds, let's delve into the specific period when birds are most receptive to these influences.

1.4 Critical period in vocal development in songbirds

The sensitive period is a time when songbirds are responsive to song stimuli and have the easiest time memorizing them. Young birds listen to other adult birds throughout their early critical period and learn songs by memorization. This critical period is essential for the acquisition and refinement of vocalizations and is characterized by two sub-phases: the auditory phase of song memorization (during which birds produce "subsong") and the motor phase of song development (when they sing "plastic song"). In the auditory phase, birds learn the specific sound patterns that they will later mimic. For instance, song sparrows (*Melospiza melodia*) can replicate memorized song phrases precisely with as few as 30 exposures to a model in a day (Peters et al., 1992), whereas nightingales (*Luscinia megarhynchos*) require only 10 exposures to produce precise copies (Hultsch & Todt, 1989).

During the motor phase of song development, birds practice and refine their vocalizations until they can accurately reproduce the learned songs (Marler & Slabbekoorn, 2004). Young birds listen to their own songs and progressively alter the songs they sing to conform to the models they have stored in their memory. In some species, the auditory and motor phases overlap, but in others, they are separated (Catchpole & Slater, 2003). Once the critical period ends, birds' ability to learn songs decreases significantly (Brainard & Doupe, 2002). Among-species variation in the critical period is responsible for the differences between open-ended and closed-ended learners.

1.5 Variability in song learning strategies: Open/Closed-ended learners

Song learning is limited to an early sensitive period known as the "critical period" in some songbird species, but not others. Species classified as closed-ended learners, like the white-crowned sparrow (*Zonotrichia leucophrys*) and the zebra finch (*Taeniopygia guttata*), have a restricted ability to learn new songs. Once the song is learned during the critical period, it becomes crystallized as birds mature. While song structure is maintained, performance can improve for a period before eventually declining (senescence), unless certain elements are lost to selective attrition (Ota & Soma, 2014). There are no additions to the song repertoire of closed-ended learners after the critical period. Cooper et al. (2012) examined age-related changes in the songs of Bengalese finches (*Lonchura striata domestica*) by comparing the song performances of older and middle-aged males. Their findings revealed that older males exhibited a decreased song tempo due to longer intervals between syllables, along with a reduction in pitch and a narrower range of frequency modulations in their song. Contrary to the traditional view that song crystallization remains fixed, Ota and Soma (2014) discovered that in male Java sparrows (*Lonchura oryzivora*), song performance improved beyond the first-year crystallization phase. Improvements were observed in motor-related aspects, such as increased song length, faster tempo, and reduced variability in note production. Given that song learning accuracy in closed-ended learners is crucial for effective communication, mate attraction, and territory defense (Marler & Slabbekoorn, 2004), these findings suggest that improvement in song performance may persist in some species.

Open-ended learners, such as the European starling (*Sturnus vulgaris*) and the canary (*Serinus canaria*), can learn new songs or modify their existing songs throughout their lives. These species have high levels of vocal flexibility, allowing them to incorporate novel elements into their repertoire even in adulthood. Open-ended learners exhibit prolonged sensitive periods of vocal plasticity, during which they actively explore and acquire new song elements. They continue to refine their vocalizations beyond the initial stages of song learning, often integrating elements from their environment into their songs (Catchpole & Slater, 2003; Marler & Slabbekoorn, 2004).

1.6 Song type preference

In this thesis, "song type preference" refers to the tendency of individual birds to sing certain song types in their repertoire more than others. Evidence from various bird species supports the widespread occurrence of song type preference. Songbirds may exhibit song type preference generally or in specific contexts (Marler & Slabbekoorn, 2004). General song type preference refers to the consistent use of specific song types across various contexts, reflecting inherent preferences often linked to functions such as reproductive success and territory maintenance. These preferences are typically stable and susceptible to influences from species-specific traits, early exposure, and genetic predisposition. Consistent use of preferred song types contributes to successful mate attraction and territorial defense (Beecher et al., 2000; Searcy & Nowicki, 2005). Contextual song-type preference is characterized by the selection of song types that vary depending on the habitat or social situation. This adaptive preference allows birds to tailor their vocalizations based on immediate needs, such as during aggressive interactions, courtship, or territory establishment. Contextual preference demonstrates flexibility in song use, as birds modify their vocal behaviour in response to specific stimuli or interactions (Amrhein et al., 2004; Otter et al., 2002). In view of this, my focus is on contextual song type preference during the dawn chorus.

1.7 Species- and dialect- specific preference

Many songbirds prefer songs of their own species or local population. Young birds exhibit an innate ability to recognize and preferentially learn conspecific songs, which helps them learn the appropriate songs for communication and mating. For example, swamp sparrows (*Melospiza georgiana*) prefer to learn song types that are characteristic of their species. Males tend to learn and sing songs with specific frequency ranges and note structures that are prevalent in their local population (Searcy & Nowicki, 2000). Juvenile male swamp sparrows learn songs that are typical of their species, preferring songs with consistent trill rates and bandwidths, which may help in species recognition and communication efficiency (Lachlan et al., 2014). Birds may have a predisposition to learn sounds that share key acoustic characteristics with their own vocalizations. Mockingbirds (*Mimus polyglottos*), for example, imitate species whose calls are acoustically similar to their own non-imitative songs (Gammon, 2013).

White-crowned sparrows (*Zonotrichia leucophrys*) exhibit preference for song types typical of their local dialect. Young males learn and incorporate prevalent local songs into their repertoires rather than less prevalent songs or songs from other dialects. When exposed to multiple dialects, young males prefer the dialect they heard most frequently during their sensitive learning period (Marler & Tamura, 1962). Species like the song sparrows (*Melospiza melodia*) have large repertoires but prefer to sing song types that are more common in their local area. Young song sparrows learn and imitate song types from their neighbours rather than unrelated adults from different populations (Beecher et al., 2000). This finding suggests that local prevalence may shape song type preferences in this species.

1.8 Repertoire size and complexity preference

In species with large and moderately sized repertoires, males do not use all song types equally across contexts. For example, house wrens (*Troglodytes aedon*) use certain song types more frequently during the mating season, suggesting that these songs may be particularly effective in attracting mates (Kaluthota, 2016). This pattern of song type use preference is not unique to house wrens, as many other species also exhibit contextual song type preference for higher mating success e.g., Eastern bluebirds (*Sialia sialia*; Gowaty & Plissner, 1998), European starlings (*Sturnus vulgaris*; Eens et al., 1991), chestnut-sided warblers (Setophaga pensylvanica; Byers, 1995); and for territorial defense e.g., chaffinch (*Fringilla coelebs*), great tit (*Parus major;* Krebs et al., 1978). In chaffinches, males use certain song types more frequently during peak singing hours, suggesting that these songs are particularly effective in maintaining territory boundaries (Marler, 1956). Similarly, in chestnut-sided warblers, males that sing more of the locally preferred song types tend to have greater mating success, reinforcing the link between song preference and reproductive fitness (Byers, 1995).

1.9 Preference during countersinging and territory defense

In some species, certain song types are consistently favoured across context, indicating a stable and broad preference that may act as a default option during aggressive interactions. For example, song sparrows (*Melospiza melodia*) use some song types more frequently regardless of the context (Beecher et al., 2000). Similarly, black-capped chickadees (*Poecile atricapillus*) also prefer certain variations of their “fee-bee” song during competitive interactions with conspecifics (Otter et al., 1999). Other species that exhibit preference for certain song types during aggressive interactions with rivals include common nightingales (*Luscinia megarhynchos*; Kunc et al., 2007), while great tits (*Parus major*) adjust their preference to match the predominant local song types when communicating with neighbours (Mcgregor & Krebs, 1982). In tropical mockingbirds (*Mimus gilvus*), some song types are commonly used during dawn chorus, a time when males are believed to be signalling their presence and reinforce territory boundary to both mates and rivals (Botero et al., 2009).

Banded wrens (*Thryothorus pleurostictus*) adjust their song preferences based on time of day, location on the territory, female presence, and singing state. While individual males strongly overused or underused some song types, they prefer to use song types shared with their neighbour during countersinging (Trillo & Vehrencamp, 2005). Similarly, male rock wrens (*Salpinctes obsoletus*) prefer to sing certain types of song types when protecting their territory and trying to attract a mate. This shows that song repertoire may be functionally differentiated (Pitt, 2018).

1.10 Song type sharing might determine neighbourhood preference

When multiple birds sing the same song type, they are said to "share" that song. Most passerines engage in some level of song type sharing, although the extent of sharing can vary substantially among populations of the same species (Beebee, 2002). In some systems, birds may preferentially sing song types because they are widely shared in the population. The prevalence of a song type in a population increases the likelihood of its transmission to subsequent generations, creating a form of social conformity. There is evidence that both male e.g., swamp sparrow (*Melospiza georgiana*; Lachlan et al.,

2018) and female receivers e.g., white-crowned sparrows (*Zonotrichia leucophrys*; Soha & Marler, 2001) prefer local song types.

1.10.1 Variations in song sharing among bird species

Males in certain species share relatively little of their repertoire with other males in their population (Ewert & Kroodsma, 1994; Kroodsma et al., 1999), whereas in others, they share almost all of it (Demko et al., 2016; Molles & Vehrencamp, 1999). For example, white-throated thrushes (*Turdus assimilis*) have a small overlap of 2% in their repertoires between any two males (Vargas-Castro, 2015). Western song sparrows share a moderate 24-34% of their repertoires with their neighbours (Hill et al., 1999), while European wrens (*Troglodytes troglodytes*) have a relatively high overlap of 40% in their repertoires (Catchpole & Rowell, 1993). The highest level of song type sharing was found in the canyon wren (*Catherpes mexicanus*), with males sharing 94% of song types (Benedict et al., 2013). Proximately, these differences in song-type sharing between species are mostly due to differences in how juvenile birds disperse and the length and timing of critical periods and selective attrition. Ultimately, they are shaped by natural selection.

The interaction between learning, dispersal, and selective attrition produces distinct song sharing patterns across species. For instance, in Washington state song sparrows, learning from neighbours results in a moderate degree of song sharing, particularly among adjacent males. This localized learning reinforces repertoire convergence among birds that remain in close proximity (Beecher et al., 1994). Conversely, in the canyon wren, limited dispersal distances result in higher song type sharing because juveniles settle near the adult song models they learned from (Benedict et al., 2013). Birds that disperse over long distances, like the white-throated thrush (Vargas-Castro, 2015), are less likely to share songs with their new neighbours because they learn songs in one area and disperse to a different area. Hence, there is minimal song sharing due to exposure to diverse song cultures and less selective attrition to bring repertoires into line with local song types.

1.10.2 Patterns of song type sharing among male songbirds

Song type sharing among male songbirds often depends on their proximity to one another. In species such as the tufted titmouse (*Baeolophus bicolor*) and village indigobird (*Vidua chalybeata*), neighbouring males frequently share most of their songs (Payne, 1985; Schroeder & Wiley, 1983). Although song sharing is often linked to geographic proximity, its extent and function vary across species and populations (Hughes et al., 1998; Niederhauser & Anderson, 2023).

For many species, song sharing is more pronounced among adjacent neighbours and decreases with increasing territorial distance. In song sparrows (*Melospiza melodia*), overlapping song repertoires are common among close territorial males, while distant individuals share few to no songs (Wilson et al., 2000). Similarly, in the Carolina wren (*Thryothorus ludovicianus*), males within the same population share about 66% of their songs, but this sharing declines as the distance between territories increases (Morton, 1987). This pattern suggests that males may be under selection pressure to learn songs that are prevalent among nearby neighbours, as song sharing plays a critical role in maintaining territoriality and reducing conflict (Beecher et al., 1994). A study on Washington song sparrows further supports this, showing that territory ownership duration is positively correlated with the number of shared songs with neighbouring males (Beecher et al., 2000).

Three distinct patterns of song type sharing have been identified (Wilson et al., 2000). Model A is characterized by a non-linear, steep decline in song sharing over distance. Neighbouring males share many song types, while non-neighbours share very few. This pattern can arise when birds learn and retain songs primarily from their immediate vicinity before migrating or when they adjust their repertoires after settling in a new area. Species that adhere to this model include the village indigobird, American redstart (*Setophaga ruticilla*; Lemon et al., 1994), and chowchilla (*Orthonyx spaldingii*; Koetz et al., 2007).

Model B is characterized by a linear decline in song sharing with distance. This pattern is expected when birds stop learning songs before dispersal and disperse varying distances, leading to gradual changes in song similarity. Species such as certain wrens, Adelaide's warblers (S*etophaga adelaidae*), and song sparrows fit into this model (Staicer, 1991; Wilson et al., 2000).

Model C is characterized by peak song sharing at intermediate distances. This model shows peak song sharing at intermediate distances with minimal sharing among immediate neighbours. This can occur when birds avoid song sharing with close neighbours by settling further away or altering their repertoires through learning or selective attrition after dispersal. Species exhibiting this pattern include the curl bunting (*Emberiza cirlus*; Kreutzer, 1987) and common nightingale (*Luscinia megarhynchos*; Hultsch & Todt, 1981).

1.11 Why songbirds might prefer certain song types

My thesis asks whether Adelaide's warbler males prefer to sing certain song types in their repertoires, and, if so, why they prefer the songs they do. I first tested whether males exhibit song type preference during the dawn chorus and whether their preferences were consistent across days. My first functional hypothesis was that males preferentially sing certain song types from their repertoire more than others because they are widely shared in the neighbourhood. If supported, this hypothesis would suggest that males align their song preferences with local social norms to facilitate better communication with male and female receivers.

I defined song type prevalence as the number of conspecific males that share a given song type(s). Male birds may preferentially sing more of the prevalent song types in their environment to align with local social norms and improve their communicative success. Prevalent song types could provide social or territorial advantages by facilitating better interaction with neighbours and increasing perceived social cohesion (Beecher & Brenowitz, 2005). Additionally, using prevalent song types may signal local adaptation or membership in the community, enhancing both territorial defense, and mate attraction.

Of course, preference for a given song type may also influence its prevalence. Individuals may independently come to prefer the same set of song types, e.g., because of their transmission characteristics (Bradbury & Vehrencamp, 2011). Over time, the accumulation of individual preferences could lead to the widespread use of certain song types, providing more models of those types for young song learners, and thus increasing their prevalence in the population (Catchpole & Slater, 2003). This interaction between song type prevalence and senders' preference could create a feedback loop, where prevalent songs reinforce their use due to social learning (Beecher & Brenowitz, 2005).

The Social Dynamic Hypothesis (SDH) suggests that male birds sing together at dawn (resulting in the "dawn chorus") to communicate and establish social bonds with their neighbours (Staicer et al., 1996). This dawn communication is particularly effective because it occurs at a time when birds are less distracted by foraging or other daily activities, allowing them to focus on social and territorial maintenance through shared songs (Gil & Llusia, 2020). This idea is consistent with the general sharing hypothesis as well, which states that males preferentially sing highly shared songs at dawn (Lapierre et al., 2011). Singing prevalent (shared) song types at dawn may reinforce social bonds among neighbouring male songbirds. During the dawn chorus, birds engage in high intensity singing. Increased song matching between neighbours frequently occurs during this early morning singing period, which may aid in reaffirming territorial boundaries and mutual recognition (Catchpole & Slater, 2003). The use of shared song types at dawn allows neighbouring males to communicate their presence and territorial stability. This early vocal signalling may serve as a non-confrontational way of maintaining the status quo, where neighbours acknowledge each other's claims through familiar song patterns rather than direct conflict, ultimately promoting social cohesion within the community (Staicer et al., 1996).

The second functional hypothesis I tested is that males prefer to sing songs with superior transmission in the environment. Songs with superior transmission will have characteristics such as lower frequencies and slow tempos that enhance their reach and clarity in the local environment. The Acoustic Adaptation Hypothesis (AAH) proposes that acoustic signals evolve to optimize transmission efficiency and detectability in the habitats in which the animal delivers the signal (Morton, 1975). Indeed, one of the reasons males sing so much at dawn may be that the dawn offers optimal conditions for sound propagation, enhancing the efficacy of long-range communication (Dabelsteen & Mathevon, 2002;

Henwood & Fabrick, 1979). If that is true, we might expect birds to prefer song types that are more effective at propagating through the environment during the dawn chorus (Morton, 1987).

Finally, I tested the hypotheses that males prefer to sing song types that require either high or low vocal performance. Vocal performance is defined as the degree of challenge to the motor system, respiratory system, or other physiological processes involved in vocalization (Byers et al., 2010; Cardoso, 2017). It may be a reliable indicator of the sender's condition to both male and female receivers (Logue et al., 2020; Podos, 1997). Trade-offs in acoustic traits are one way to assess the limits of vocal performance. Vocalizations that approach or exceed empirically derived performance thresholds are considered high performance, while those that are distant from the threshold are low performance (Logue et al., 2020). Vocal performance measurements obtained through this method are referred to as "vocal deviations" (Podos, 2001). Low vocal deviation scores indicate high song performance as the bird is closer to the performance limit and vice versa (Podos, 1997).

Scientists use vocal performance to describe several elements of singing behaviour at various organizational levels, ranging from the amount of time spent singing to consistency in duration or frequency across similar song types (Byers, 2007; Gil & Llusia, 2020). If song types vary in performance requirements, then a male's song performance depends on the song types it chooses to sing (Logue & Forstmeier, 2008). Variations in song type use among dark-eyed juncos (*Junco hyemalis*) indicate that certain songs may be preferred due to their high-performance requirements. This suggests that male quality could potentially be communicated through their song performance, as different birds may choose to sing specific song types based on their individual capabilities and strengths (Cardoso et al., 2009). That finding is compatible with the hypothesis that males prefer to sing challenging song types to show off their singing ability. However, the opposite hypothesis is also reasonable: Males may prefer song types with low performance requirements to avoid expending too much energy or pushing the limits of their singing physiology.

Songbirds often choose to sing certain song types more than others, but few studies have investigated the causes of song type preferences. This project aims to improve our understanding of song type preferences in male Adelaide's warblers. These findings will offer valuable insights into why males prefer certain song types and, ultimately, why song type repertoires evolve.

CHAPTER 2: FIELD METHODS AND DATA PREPARATION

2.1 Adelaide’s Warbler

Adelaide’s warbler (*Setophaga adelaidae*) is a small, insectivorous, socially monogamous, year-round territorial, tropical songbird endemic to the Caribbean Island of Puerto Rico. It is characterized by its bright yellow underparts, olive-green upperparts, and distinctive facial markings, including a white eye-ring and a yellow stripe above the eye. This species is a member of the New World Warbler family (Parulidae), known for their vibrant plumage and melodious songs. Male Adelaide warblers have a repertoire of about thirty song types, composed of frequency-modulated trills, which they learn by imitation. Each male’s repertoire comprises two categories, A and B, characterized by distinct delivery times, song rates, and song switching frequencies.

After dawn, all year round, males sing Category A songs in repeat mode, with extended silent intervals between songs. Adelaide warblers are one of many species of warblers that sing the dawn chorus made up exclusively of Category B songs (Staicer et al., 1996). During the dawn chorus, which is the focus of this study, males sing in switch mode (i.e., moving from one song type to another), with short breaks between songs. Different males can use the same song type in either category, so Category A and B songs have similar overall song structures. However, thorough analyses of A versus B songs revealed minor structural variations (Kaluthota et al., 2019; Staicer et al., 1996).

Figure 2.1: David M. Logue extracting a male Adelaide's warbler from the mist net in its habitat. Photo credits: Tanya Martinez.

Understanding the geography of song type sharing is important not only because it provides clues about song learning but also because sharing influences communication among neighbouring males. Adelaide's warblers' population is characterized by moderate to high song type sharing among neighbours, which decreases linearly with distance. Males typically share many song types with their closest neighbours, and then song type sharing declined with increasing distance between males (Staicer, 1991; Wilson et al., 2000).

Adelaide's warblers are ideal species for this study because they sing a lot during the dawn chorus, possess a discrete yet relatively large song type repertoire, and there is anecdotal evidence that individuals prefer certain song types. Because they share song types with neighbours, I can use them to test whether local prevalence influences preference. Additionally, they have been the subject of our lab's long-term research on vocal interaction, song type use, and vocal performance.

2.2 Data Collection

2.2.1 Study Site

A seven-person field crew studied a population of Adelaide's warblers at the Cabo Rojo National Wildlife Refuge (US Fish and Wildlife Service; 17.98° N, 67.17° W) in western Puerto Rico from April 25 to May 24, 2022. This secondary growth tropical dry forest is characterized by deciduous vegetation with a low (usually < 6 m) open canopy and an understory comprised of grasses and shrubs (Pereira-Castañeda, 2013). The average annual rainfall is 1000 mm. The birds in our study had territories located in riparian zones adjacent to seasonal streams (Weaver & Schwagerl, 2009). The study dates are within the population's breeding season (Spector, 1991).

2.2.2 Marking birds

The crew first determined which males in the study area were already banded from previous field seasons. They captured unbanded males with acoustic lures and mist nets and fitted them with unique combinations of plastic-coloured leg bands and U.S. Fish and Wildlife Service metal leg bands for identification.

2.2.3 Mapping

The field crew then mapped territories and determined the locations of the trees in which males sang during the dawn chorus ("dawn trees"; Fig. 2.1). When they observed a banded bird singing at any time of day, they took its latitude and longitude with a GPS unit (Garmin GPSmap 64 or 64s) set to "waypoint averaging" to increase precision. The crew used the locations to map territory borders and dawn trees in Google Earth Pro v. 7.3 (Google LLC, Mountainview, CA). They continued adding new locations throughout the study. Recordists loaded updated map files onto their cellular telephones each day.

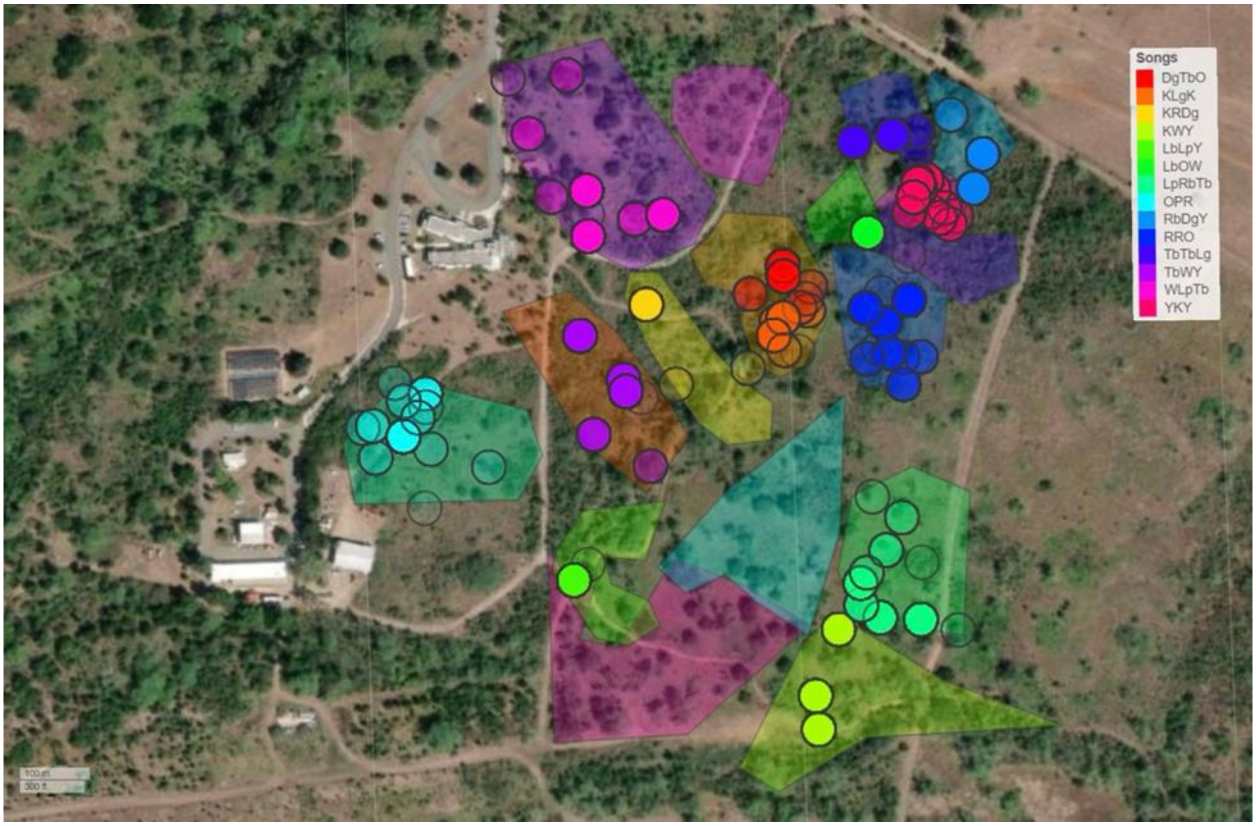


Figure 2.2: Map of Cabo Rojo National Wildlife Refuge showing the territory of individual males in different colours. Circles symbolize a location where a male sang during the dawn chorus recordings. Opacity indicates song count. Polygons show the limits of the territory. Territory corners are song posts observed before and during the recording period.

2.2.4 Recording

The study area was divided into three “neighbourhoods,” each comprising six neighbouring territories. The crew recorded the South Neighbourhood May 9–12, the North Neighbourhood May 13, 14, and 16–18, and the Central Neighbourhood May 19–21, 23, and 24. Recordings were made with Sennheiser ME66 shotgun microphones and Marantz PMD-661 digital recorders (file format = wav, sampling rate = 44.1KHz, bit depth = 16 bits, automatic level control = on). To begin each recording session, the six recordists assembled at the field site 45 minutes before dawn, began recording, and pointed their microphones at the coordinator, who stated the exact time and sounded a dog clicker. The click would later be used to synchronize the recordings.

Prior to the onset of the dawn chorus, each of the six recordists proceeded to the dawn tree of the focal male that was assigned to them. The Google Earth Pro app (Google, 2021) on their phones allowed them to see their own current location as well as the locations of the territory borders and dawn trees. Each recordist attempted to record all songs from their focal male. They acoustically marked songs from the focal male with the word "mine." Other common verbal notes included changes in the bird's location, comments on behaviour, "not my bird" when a nearby non-focal bird sang, and "off bird" when the recordist lost their focal bird. The recordists used binoculars (Vortex Diamondback HD 8 x 42; Vortex Optics, Barneveld, WI) to visually confirm the identity of the focal male by the end of each recording session. Recordings ended no earlier than 700 seconds after dawn to ensure they captured the entire dawn chorus.

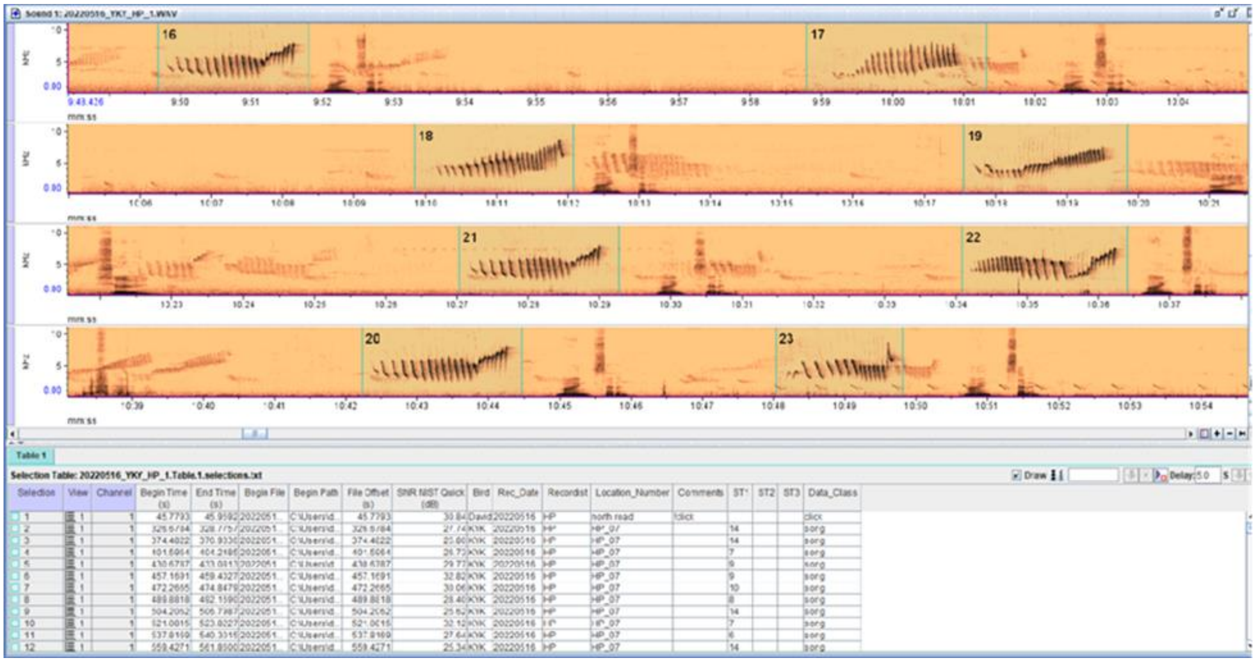
2.2.5 Ethics and Permits

This study adheres to the guidelines from the Animal Welfare Committee at the University of Lethbridge (protocol #2006). It also follows the ASAB/ABS Guidelines for the use of animals in research (Society, 2003). Fieldwork was conducted with permission from the U.S. Fish and Wildlife Service (permit # 41520-2022-07) and the Departamento de Recursos Naturales y el Medioambiente (permit # 01273-09). Bird handling was conducted under David M. Logue's master bird banding license (permit # 23969).

2.3 Scoring Recordings

2.3.1 Scoring song types

The recordings were promptly transferred to cloud storage and annotated on the same day they were created to minimize the risk of scoring errors. Four trained scorers (David M. Logue, Heath Petkau, Juleyska Vazquez-Cardona, and Samantha Huang) scored the recordings in Raven Pro 1.6 (Yang & Bioacoustics, 2019; Spectrogram settings: Window size = 512 points, Window shape = Hann, overlap = 50%). This initial round of scoring indicated the timing and location of each song and other behavioural data. Later, one scorer (David M. Logue) scored song types for each bird while building song type repertoires (Figs. 2.3, 2.4). At this point, song types were only scored within individuals ("individual song types” or ISTs), so song type repertoires could not be compared among individuals. It was still necessary to build a “universal song type” (UST) key to compare repertoires among birds.



Selection Table: 20220516_YKY_HP_1.Table.1.selections.txt

Selection	View	Channel	Begin Time (s)	End Time (s)	Begin File	Begin Path	File Offset (s)	SNR NIST Quick (dB)	Bird	Rec_Date	Recordist	Location_Number	Comments	ST1	ST2	ST3	Data_Class
1	1	1	45.7793	45.9592	2022051...	C:\Users\d...	45.7793	30.84	David	20220516	HP	north road	fclick				click
2	1	1	326.5784	328.7757	2022051...	C:\Users\d...	326.5784	27.74	KYK	20220516	HP	HP_07		14			song
3	1	1	374.4022	376.9336	2022051...	C:\Users\d...	374.4022	25.60	KYK	20220516	HP	HP_07		14			song
4	1	1	401.5064	404.2186	2022051...	C:\Users\d...	401.5064	26.73	KYK	20220516	HP	HP_07		7			song
5	1	1	430.6787	433.0813	2022051...	C:\Users\d...	430.6787	29.77	KYK	20220516	HP	HP_07		9			song
6	1	1	457.1691	459.4327	2022051...	C:\Users\d...	457.1691	32.82	KYK	20220516	HP	HP_07		9			song
7	1	1	472.2665	474.8479	2022051...	C:\Users\d...	472.2665	30.06	KYK	20220516	HP	HP_07		10			song
8	1	1	489.8818	492.1590	2022051...	C:\Users\d...	489.8818	28.40	KYK	20220516	HP	HP_07		8			song
9	1	1	504.2062	506.7987	2022051...	C:\Users\d...	504.2062	25.62	KYK	20220516	HP	HP_07		14			song
10	1	1	521.0015	523.8227	2022051...	C:\Users\d...	521.0015	32.12	KYK	20220516	HP	HP_07		7			song
11	1	1	537.8169	540.3315	2022051...	C:\Users\d...	537.8169	27.64	KYK	20220516	HP	HP_07		6			song
12	1	1	559.4271	561.8500	2022051...	C:\Users\d...	559.4271	25.34	KYK	20220516	HP	HP_07		14			song

Figure 2.3: Sound spectrogram in Raven.

Jade Nelson and I developed a universal song type key for the lab using blind scoring. Working independently, we visually compared the songs in each male’s repertoire with the song in every other male’s repertoire and labelled song type dyads as identical (>90% similar), similar (70-90% similar), and different (<70% similar). When both scorers agreed, our labels stood. Where we disagreed, a third observer (D.M.L.) determined the label. For the present analysis, we took a conservative approach and treated “similar” dyads as “different”.

Our lab developed a novel network-based approach to classify song types among males. We made a non-directional, unweighted network in which each song type from each male was a node, and perfect matches were edges. We treated each component from this disconnected network as a distinct song type. We call these “universal song types” (USTs) to distinguish them from the within-individual male song types (ISTs).

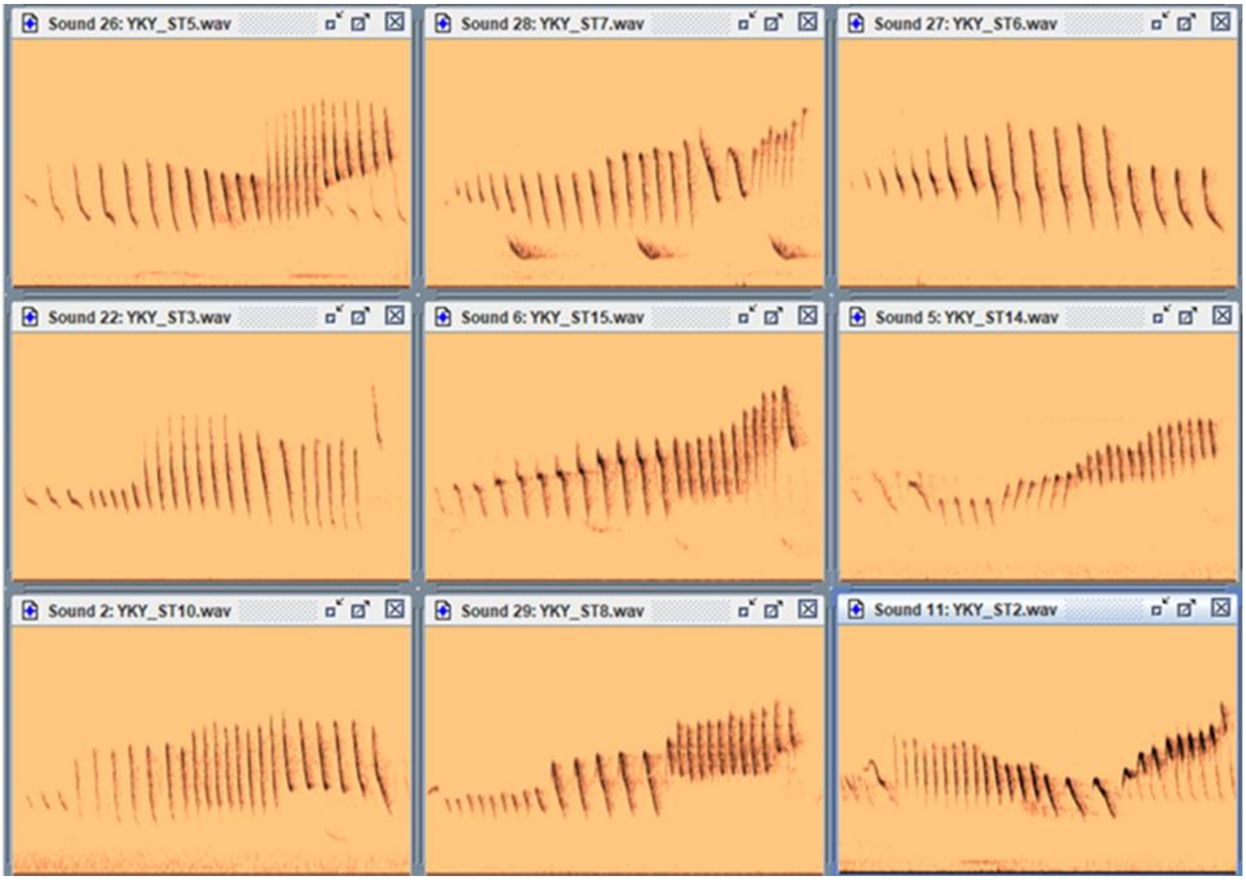


Figure 2.4: Spectrograms showing a portion of the song repertoire of male YKY

2.3.2 Processing Data

We conducted data processing and analysis in R version 4.3.0 (Team, 2020) running in the R Studio (Team, 2024) integrated development environment. Selection tables from Raven were imported into R with the *imp_raven* function from *Rraven*. One person (David M. Logue) checked for and corrected errors and used the click to synchronize the day's recordings with one another and with the local time.

2.3.3 Acoustic Analysis

We conducted automated acoustic analyses in R. We first used the R library *WarbleR* (Araya-Salas & Smith-Vidaurre, 2017) to make an extended selection table that combines our cleaned and organized data with wav files of the corresponding song recordings. Prior to acoustic analysis, we filtered out songs that were too quiet (rms amplitude ≤ 3.0 Pa). Filtering created a second, smaller dataset comprising song recordings that were loud enough to be amenable to acoustic analysis. We used functions from *seewave* (Sueur et al., 2008) to trim off the buffer before and after each song and measure the following acoustic variables: amplitude (rms), percent sound (100 * total note duration / song duration), frequency bandwidth (maximum frequency / minimum frequency; Cardoso & Atwell, 2016), mean frequency (sum(frequency bin * amplitude / total amplitude)), and trill rate ((note count – 1)/ (song duration – duration of last note; Bradbury & Vehrencamp, 2011). We excluded the final note from the trill rate calculation because trill rates based on the full song necessarily omit the 'gap' after the last note, biasing estimates upward for songs with fewer notes. We then generated vocal deviation scores to measure trill performance. We used *lqmm* (Geraci, 2014) to conduct mixed double quantile regression (Cardoso, 2019) on the variables trill rate and frequency bandwidth (Fig. 2.5). We included ID as a random variable. We calculated deviation scores as the orthogonal distance from the regression line for both orientations of the regression. We then averaged the deviation scores from the two orientations.

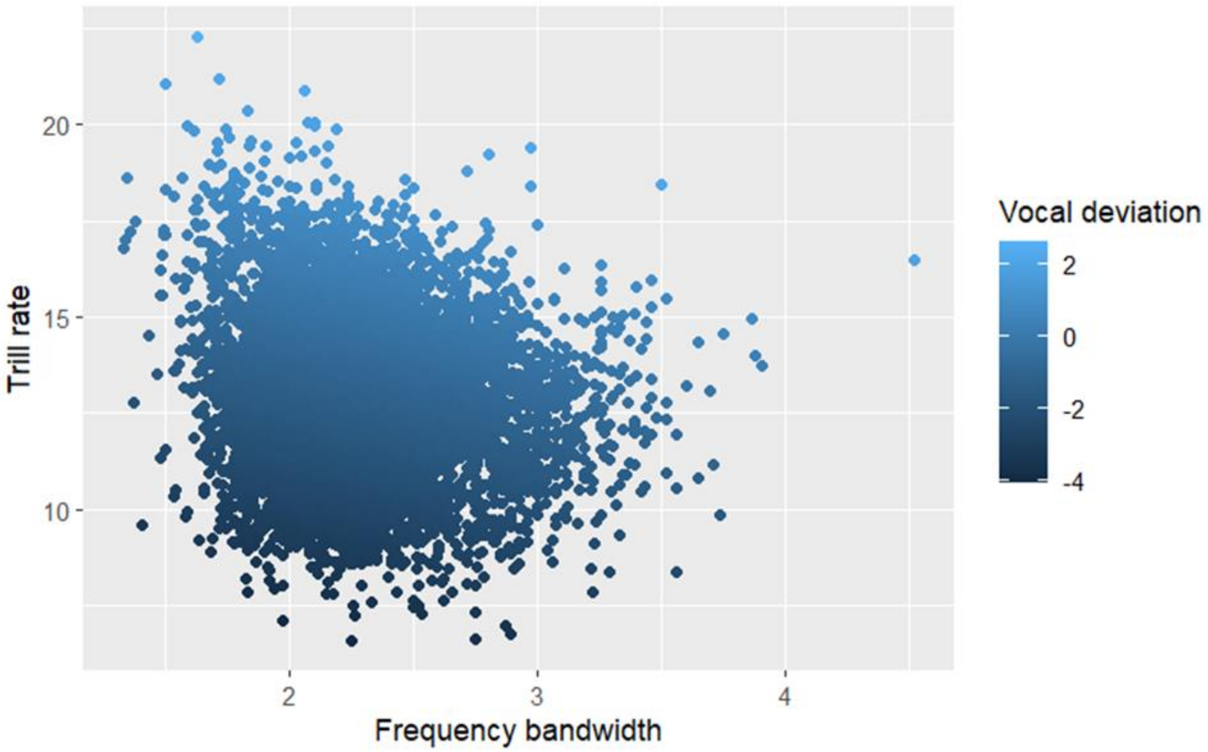


Figure 2.5: A scatter plot of frequency bandwidth versus trill rate showing the vocal deviation scores derived from mixed double quantile regression.

CHAPTER 3: DATA ANALYSIS AND RESULT

3.1 Hypotheses and predictions

3.1.1 Does song type preference exist, and is it consistent?

This study aimed to examine male Adelaide's warbler song preferences during the dawn chorus and the underlying factors that influence these preferences. I first tested whether male Adelaide’s warblers preferentially sing certain song types from their repertoires. If they did, I predicted that the observed distributions of song type use would deviate from a uniform distribution (i.e., some song types would occur more than others). I then tested whether their preferences were consistent across days. Specifically, I tested the prediction that song type predicted the number of repetitions that a male would sing across days. Based on prior observations, I expected that male Adelaide's warblers would exhibit consistent song preferences across days.

3.1.2 Song prevalence and preference

I also investigated why males prefer certain song types. I tested the hypothesis that males prefer song types that are prevalent (i.e., widely shared) within the local population. One of the reasons we might expect males to prefer prevalent song types is females’ preference for locally prevalent song types, thus leading males to prefer them. By preferring to sing locally common song types, males may ensure that their songs are easily recognized and assessed by females, facilitating mate choice (Fujii et al., 2022). Another idea is that song types shared by many other local males may signal social connectedness or familiarity, thus facilitating communication within the local acoustic environment. Males may also prefer widely shared song types because locally common song types may help with territory establishment and maintenance. If a male sings uncommon song types, he may be perceived as an outsider, triggering heightened aggression from territory-holding males (Beecher et al., 2000). If males prefer prevalent song types, I predicted that the number of males that share a song type would be predictive of individuals’ preference for that song type.

3.1.3 Transmission qualities and preference

Some song types may become widespread because they are better suited to the acoustic properties of the local environment. Songs that propagate effectively in the environment may be more likely to be adopted and maintained within the population (Derryberry, 2009). I hypothesized that males prefer song types with acoustic structures that minimize signal degradation during transmission. The three main forms of signal degradation during propagation are overall attenuation (due to spreading loss, scattering, and heat loss), frequency distortion (heat loss and scattering), temporal distortion (reverberation and echoes), and noise masking (background noise, Bradbury & Vehrencamp, 2011). Based on the hypothesis that males prefer song types that transmit through the environment efficiently, I predicted they would prefer song types with low mean frequencies (better for long distance transmission due to less attenuation by obstacles like vegetation and atmospheric conditions), low vocal deviation (low trill rates minimize temporal distortion), low percent sound (longer gaps or pauses within the song, which reduces temporal distortion), and high amplitude (loud and therefore can be heard over greater distances; Table 3.1).

3.1.4 Vocal performance and preference

It is not clear whether birds should favour song types with high or low performance during the dawn chorus. High performance songs may intimidate rivals or attract females. However, low performance song should be easier to sing and so may be preferred in contexts where high performance is not required. If males prefer high performance songs, I predicted that males would prefer songs with high vocal deviation, which is a measure of how well a bird performs its song in terms of the trade-off between fast trill rate and wide frequency bandwidth (Podos, 1997). I also predicted that males would prefer songs with a high percent sound, also referred to as acoustic density. Percent sound refers to the proportion of time a bird is actively producing sound during singing, relative to the total duration of its song performance. It is often used as an indicator of vocal efficiency and respiratory performance in birds. Logue et al. (2020) examined various metrics to assess vocal performance in male Adelaide's warblers at the note level and found that percent sound is strongly correlated with the performance metric "recovery time," which measures the duration of silent gaps following notes. A high percent sound means that a bird is spending more time vocalizing and less time pausing for breath, suggesting greater control over respiration and sound production. If birds prefer song types that require low performance, I expect the opposite pattern: they would prefer songs with low percent sound, low amplitude, and high vocal deviation (Table 3.1).

3.2 Analyses

Statistical analyses were carried out in R Studio (Team, 2024). Packages used in the statistical analysis for both data management and visualization include *dplyr* (Wickham et al., 2023), *ggplot* (Wickham, 2016), *cowplot* (Wilke, 2024), *lme4* (Bates et al., 2015), *stringr* (Wickham, 2023), *brms* (Bürkner, 2017, 2018, 2021), *dagitty* (Textor et al., 2016), and *forestplot* (Gordon & Lumley, 2023).

Table 3.1: Prediction summary used to test functional hypotheses about song type preferences

Hypothesized driver of preference	Number of neighbours that share the song type	Mean frequency	Percent sound	Amplitude	Vocal deviation
Prevalence	High	No prediction	No prediction	No prediction	No prediction
Transmission	No prediction	Low	Low	High	Low
High performance	No prediction	No prediction	High	High	High
Low performance	No prediction	No prediction	Low	Low	Low

3.2.1 Song type preference

I used the full data set (n = 11,800 songs, Table 3.2) to test this hypothesis. The sampling unit was the song type, and each male was analyzed separately. First, I made a uniform distribution for each male. A uniform distribution is a probability distribution where all outcomes are equal. I created the uniform distribution by dividing the number of songs a male sang by the number of song types in his repertoire and entering that number as the expected value for each song type. To determine if males have song type preferences, I compared the observed distribution of song types to the expected uniform distribution for each male using the chi-squared test. If the test was statistically significant, I concluded that males preferred some song types over others. I also visualized the distribution of song type use for each male with a histogram (Fig. 3.1; Appendix 1).

On average, the most common song type in a male's repertoire comprised 17% of his song output as compared to 4.75% that would be expected in the absence of song type preferences. Chi-squared tests revealed that all males demonstrated song type preference (Table 3.2). The histograms also revealed strong evidence of preferences (Fig. 3.1; Appendix 1).

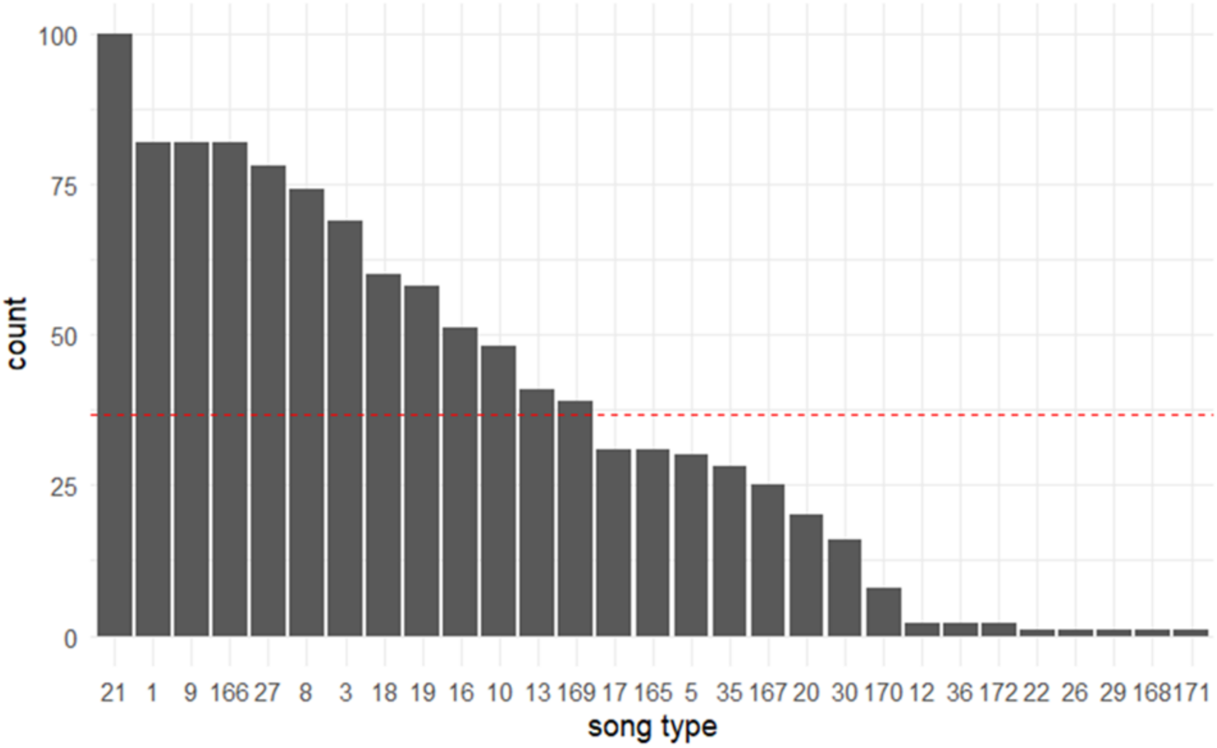


Figure 3.1: A histogram showing the distribution of song types recorded from male YKY. The red broken lines represent the expectation under a uniform distribution. Histograms for all males are presented in Appendix 1.

Table 3.2: Data summary for the full dataset that I used to test the first two hypotheses and results of the chi-squared tests for song type preferences.

Bird ID	Songs	Days	Song Types	Chi^2	df	p
YKY	1064	5	29	1498.74	28	< 0.0001
WLpTb	481	3	21	484.25	20	< 0.0001
TbWY	604	5	17	1121.45	16	< 0.0001
TbTbLg	734	5	19	377.85	18	< 0.0001
RbDgY	656	3	21	918.35	20	< 0.0001
RRO	535	5	19	1526.15	18	< 0.0001
OPR	924	5	21	2311.36	20	< 0.0001
LpRbTb	539	4	20	728.23	19	< 0.0001
LbOW	728	4	19	1638.08	18	< 0.0001
LbLpY	617	4	20	3642.05	19	< 0.0001
KWY	440	3	22	1167.00	21	< 0.0001
KRDg	1060	5	26	1500.18	25	< 0.0001
KLgK	1151	8	19	1426.33	18	< 0.0001
DgTbO	2267	10	29	8352.00	28	< 0.0001

3.2.2 Consistency of preference

This analysis used the same set of songs as the previous one. The independent sampling unit was the song type, within male, within day (n = 1089). The Bayesian generalized linear mixed model is a useful tool for analyzing data when the same individuals are measured repeatedly.

We developed the following linear model of daily song type use:

songs ~ ST + (1|ID) + (1|IST)

Where # song is the number of songs of a particular song type sung by a focal male in a day, ST is the song type, ID is male identity, and IST is the "individual's song type," which is a combination of ID and song type (e.g., YKY_21). The purpose of the term ST is to account for the effect of song type on count (do males overall sing some types more than others?). The random term for ID tells us whether males vary in the number of songs they sing. The random term for IST tells us whether individuals consistently prefer certain song types across days. I used weak prior probabilities, such that the model assumed no effects before training (normal distribution, μ = 0 ± 1). I tested the model fit with a posterior predictive check. Based on the hypothesis that preferences are consistent over days, I predicted IST will have a strong effect in the model. I also plotted the count of nine of each male's song types over the recording days to visualize song type use over time (Fig. 3.3; Appendix 3).

The posterior predictive check showed a good fit, and the r-hats and effective sample sizes indicated model convergence and adequate sampling, respectively. The model explained more than half of the variance in #songs, although much of that variance was explained by the random variables (conditional $r^2 = 0.55$; $CI_L = 0.49$, $CI_U = 0.60$; marginal $r^2 = 0.23$; $CI_L = 0.16$, $CI_U = 0.31$). The random term IST accounted for a large amount of variance (sd = 0.66; $CI_L = 0.56$, $CI_U = 0.77$), indicating that individual preferences are consistent across days. Full model results are in Appendix 2.

Forest plots of IST estimates from the model show evidence of variation in use among ISTs within days (Fig. 3.2; Appendix 2). Similarly, the line graph shows that while the frequency of song type use varied across days, use was broadly consistent within type (Fig. 3.3; Appendix 3). The posterior predictive check in the consistency of preference analysis is in Appendix 5.

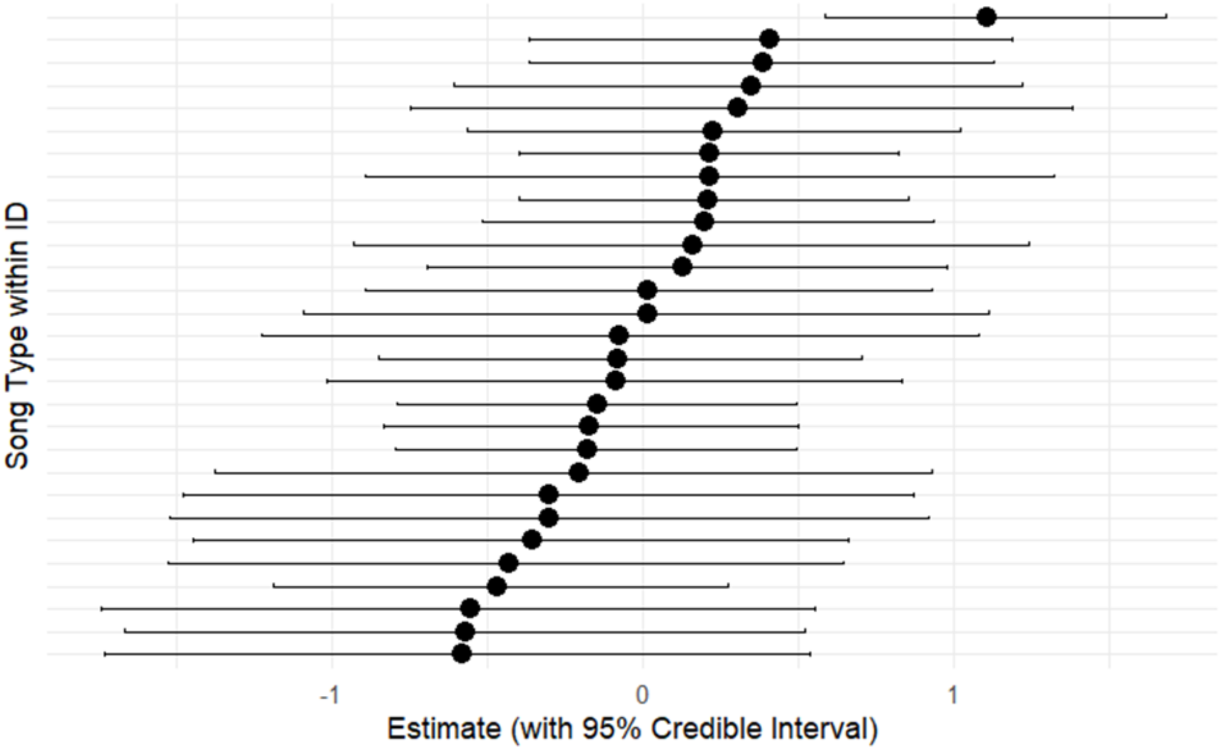


Figure 3.2: A forest plot of song type use for male YKY. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals. See appendix 2 for other males.

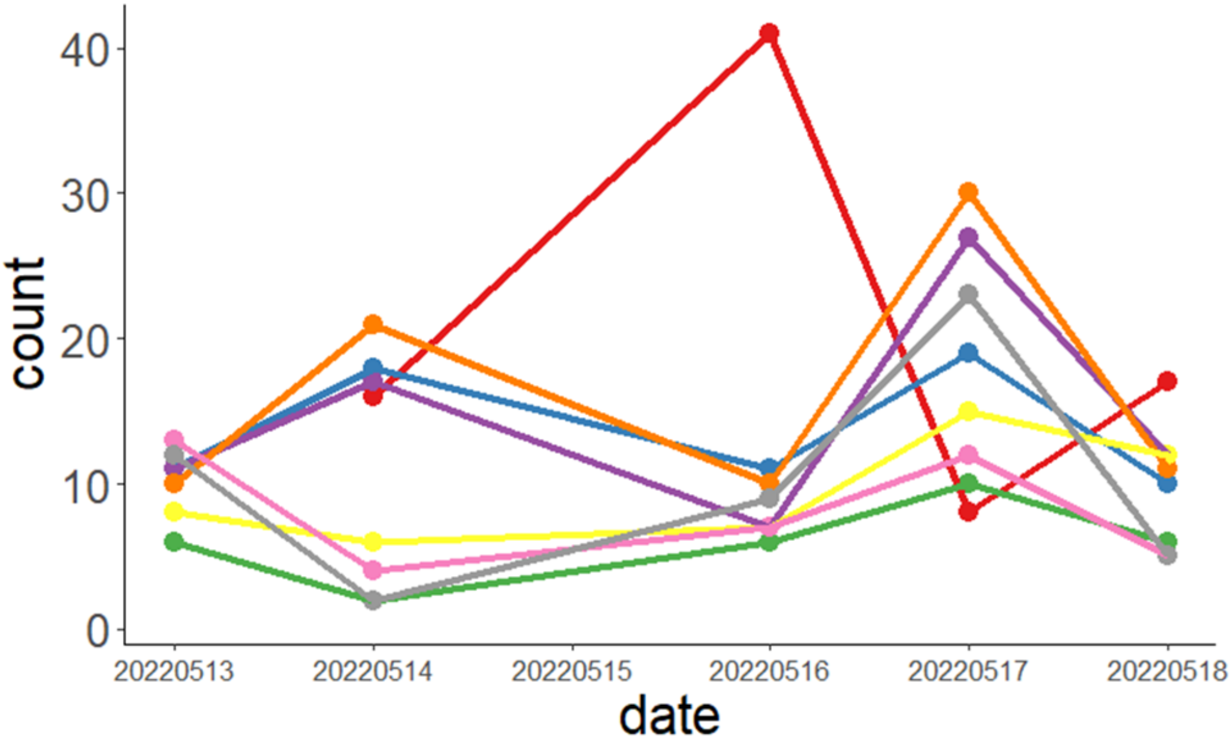


Figure 3.3: A line graph showing the count of nine of male YKY's song types over six days. Each colour represents a different song type. See appendix 3 for other males.

3.2.3 The effects of prevalence, transmission, and performance on song type preference

I made one model to test predictions of all three of these hypotheses. This analysis uses the reduced dataset (n = 9395 songs, Table 3.3), which omits song recordings that were not amenable to acoustic analysis. The sampling unit is song type within male (IST; n = 270).

Table 3.3: Data summary for the reduced dataset that we used to test the functional hypotheses.

Bird ID	Songs	Song Types
YKY	965	24
WLpTb	456	21
TbWY	533	15
TbTbLg	544	18
RbDgY	586	20
RRO	315	17
OPR	770	20
LpRbTb	405	19
LbOW	333	15
LbLpY	614	20
KWY	220	15
KRDg	839	24
KLgK	1091	19
DgTbO	1724	23

The model was structured like this:

songs ~ prevalence + avg_mean_freq + avg_percent_sound + avg_rms + avg_dev + (1|ID) + (1|UST)

Where # song(s) is the number of times a focal male sings a given song type (summed over all days in the sample) and prevalence is the number of individuals in our sample that sing that ST. The acoustic variables characterized were as follows:

average mean frequency (avg_mean_freq),

average percent sound (avg_percent_sound),

average amplitude (avg_rms), and

average vocal deviation (avg_dev).

Prior to analysis, all acoustic variables were scaled and centred to facilitate model convergence and interpretation of effect sizes. The random terms (1|ID) and (1|UST) account for male ID and song type, respectively. I used weak prior probabilities, such that the model assumed no effects before training (normal distribution, $\mu = 0 \pm 1$).

The posterior predictive checks showed that the predictions fit the data well. The r-hats and ESS values indicated convergence and adequate sampling, respectively. The model explained over 80% of the variance in song type use (conditional $R^2 = 0.82$, $CI_L = 0.81$, $CI_U = 0.84$; marginal $R^2 = 0.32$, $CI_L = 0.05$, $CI_U = 0.51$).

It indicated a strong positive effect of prevalence on individual preference (estimate = 0.83, $CI_L = 0.39$, $CI_U = 1.29$; Table 3.4; Fig. 3.4), which suggests that males prefer prevalent (widely shared) song types.

Average mean frequency (estimate = -0.46, $CI_L = -0.53$, $CI_U = -0.39$; Table 3.4; Fig. 3.5) and average percent sound (estimate = -0.23, $CI_L = -0.29$, $CI_U = -0.17$; Table 3.4; Fig. 3.6) were both moderately negatively associated with preference. That is, males tended to prefer song types that had low average frequencies and low percent sound. I did not detect any effect of amplitude (estimate = 0.01, $CI_L = -0.11$, $CI_U = 0.13$; Table 3.4; Fig. 3.7) or vocal deviation (estimate = -0.02, $CI_L = -0.10$, $CI_U = 0.05$; Table 3.4; Fig. 3.8) on preference.

Table 3.4: Relationship between predictors (prevalence) and outcomes (frequency of use/count)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**
Intercept	3.19	0.26	2.66	3.67
Prevalence	0.83	0.23	0.38	1.31
Average mean frequency	-0.46	0.03	-0.53	-0.40
Average percent sound	-0.23	0.03	-0.29	-0.17
Average amplitude	0.01	0.06	-0.11	0.13
Average vocal deviation	-0.02	0.04	-0.09	0.05

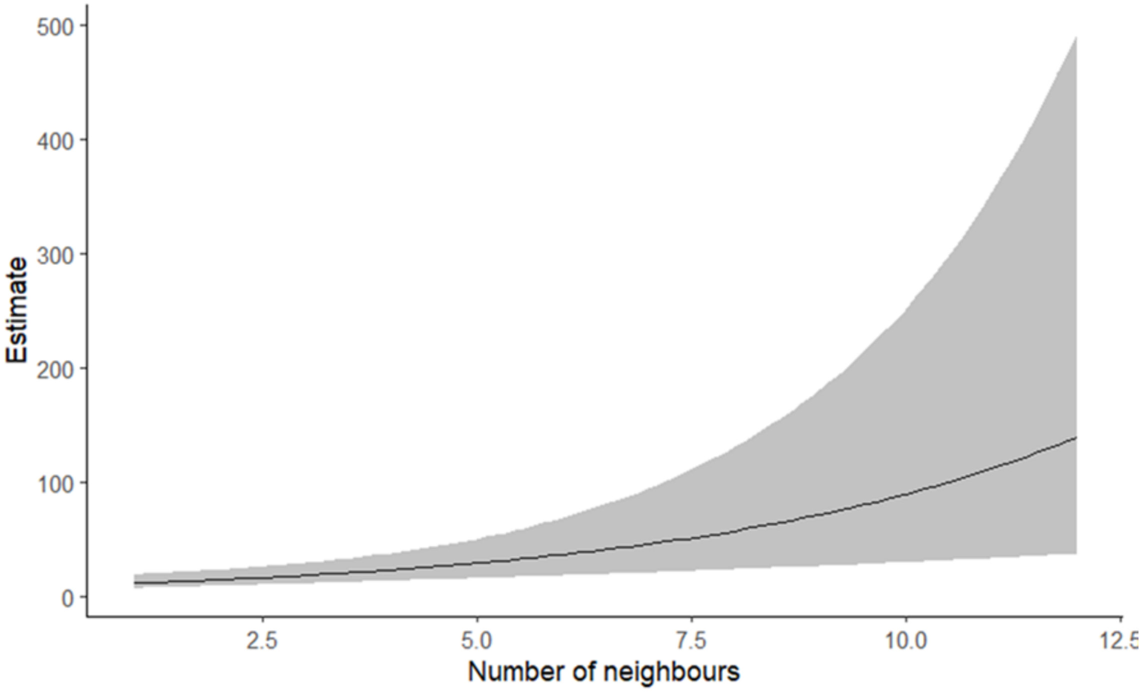


Figure 3.4: The estimated relationship between song type prevalence and song type preference in a population of male Adelaide's warblers. The black line represents the estimate, and the gray area is the 95% credible interval. See text for details.

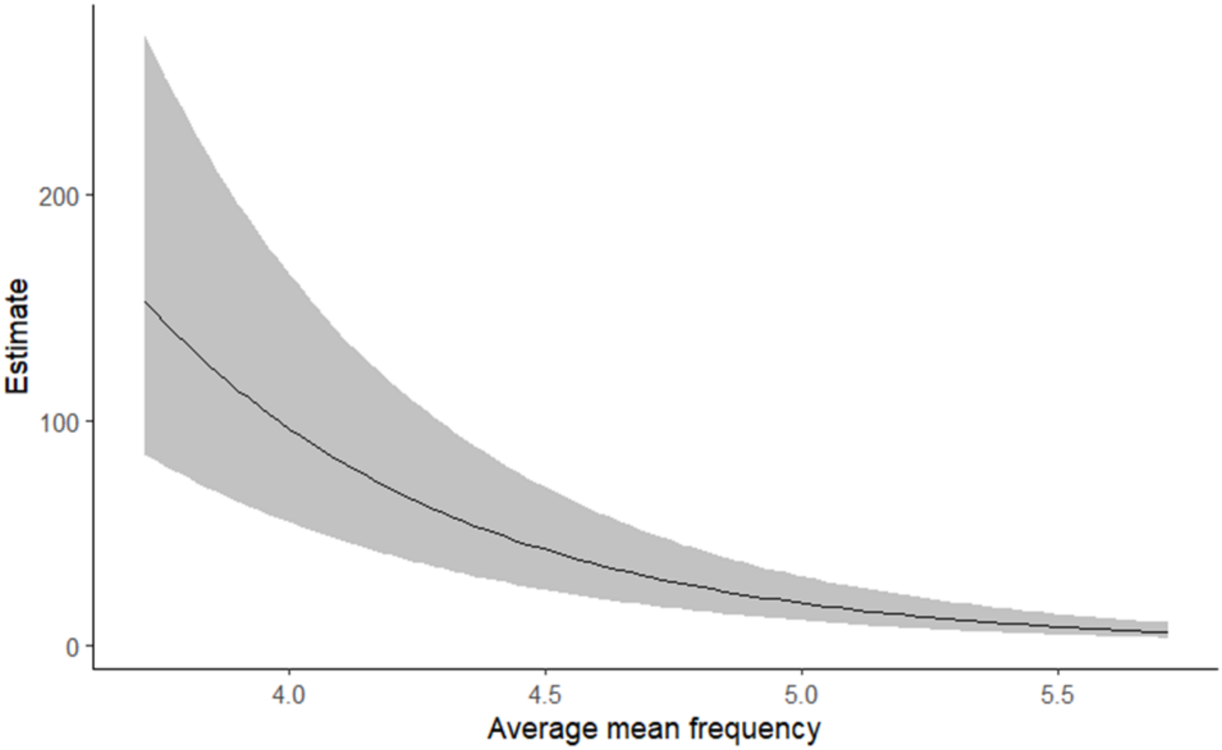


Figure 3.5: The estimated relationship between song type mean frequency and song type preference in a population of male Adelaide's warblers. The black line represents the estimate, and the gray area is the 95% credible interval. See text for details.

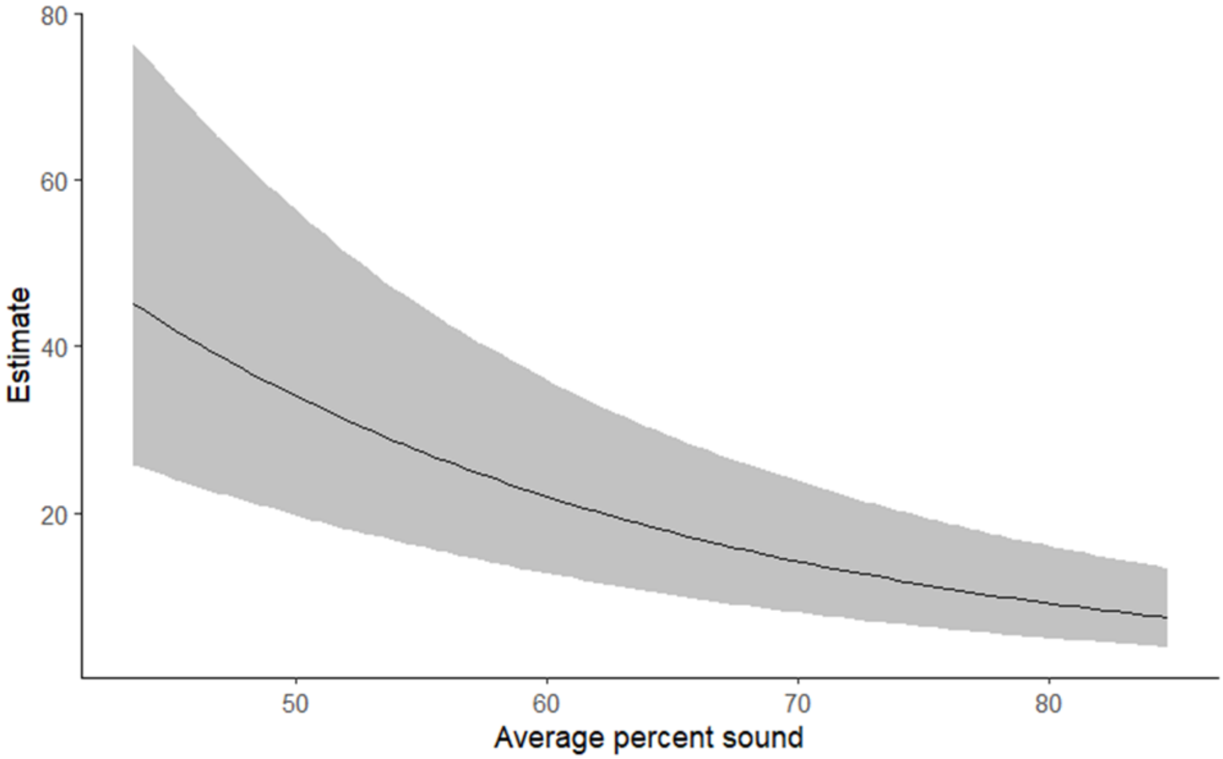


Figure 3.6: The estimated relationship between percent sound and song type preference in a population of male Adelaide's warblers. The black line represents the estimate, and the gray area is the 95% credible interval. See text for details.

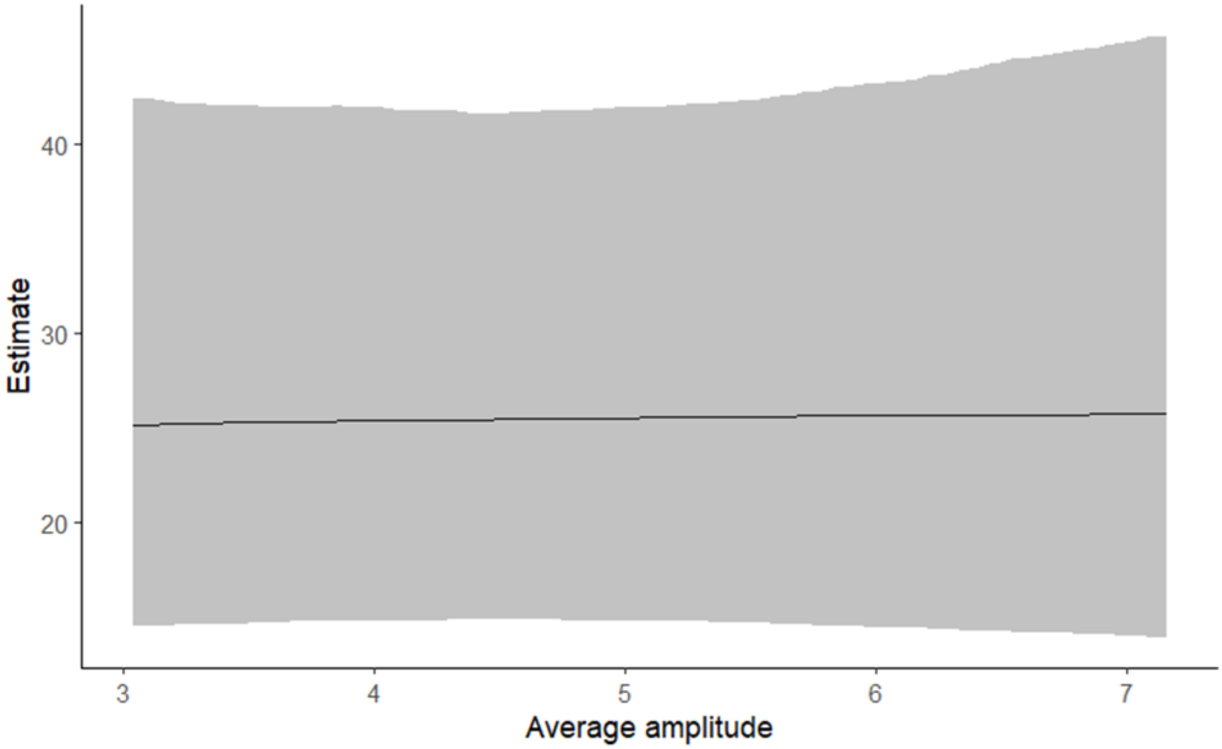


Figure 3.7: The estimated relationship between amplitude and song type preference in a population of male Adelaide's warblers. The black line represents the estimate, and the gray area is the 95% credible interval. See text for details.

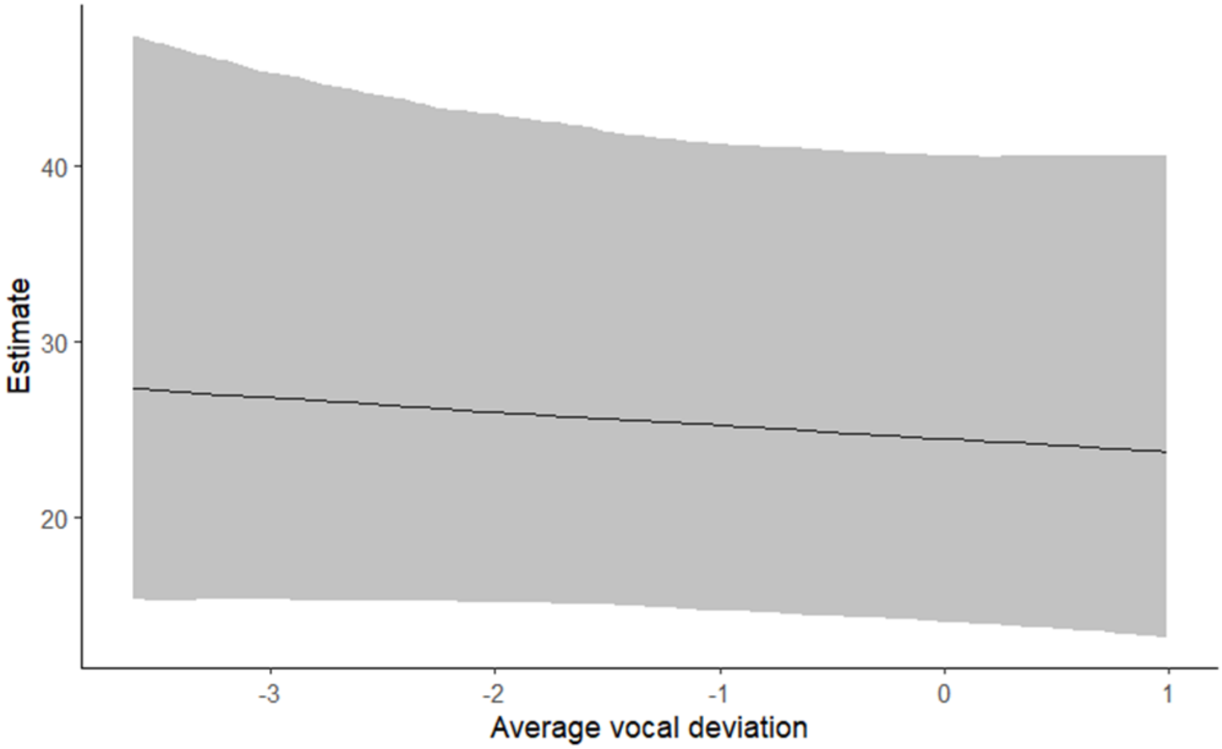


Figure 3.8: The estimated relationship between vocal deviation and song type preference in a population of male Adelaide's warblers. The black line represents the estimate, and the gray area is the 95% credible interval. See text for details.

CHAPTER 4: DISCUSSION AND CONCLUSION

4.1 Discussion

This study revealed clear evidence of song type preferences during the dawn chorus in male Adelaide's warblers. Individuals' preferences were largely consistent across days. The best predictor of individuals' preference for a song type was its local prevalence – songs that were widely shared were sung more than songs that were not. Preferences for transmission properties were somewhat supported as the preferred song types had low mean frequency and low percent sound, as predicted. However, the negligible effect of amplitude and vocal deviation on preference were contrary to my predictions. Males preferred song types with low percent sound supporting one prediction of the hypothesis that they prefer low performance song types. The predictions about amplitude and vocal deviation, however, were not supported. I found no evidence to suggest a preference for song types that require high vocal performance.

4.1.1 Males exhibit song type preferences

The male Adelaide's warblers in our sample sang some song types in their repertoire more than others during the dawn chorus (Fig. 3.1; Table 3.2; Appendix 1). While all males exhibited preferences, the magnitude of preference varied among individuals, suggesting individual variability in strength of preference. Adelaide's warbler is among the few songbird species that have been confirmed to show a preference for specific song types. Benedict and Warning (2017) explored the possibility of adaptive song type use in rock wrens (*Salpinctes obsoletus*) and discovered that the frequency of use varied among individuals, with certain song types being more prevalent than others. This is an indication that rock wrens exhibit preference. Individual male Cozumel wrens (*Troglodytes aedon beani*) prefer certain syllables, incorporating them more frequently into their vocalizations (Sosa-López & Mennill, 2014b). The selective use of specific syllables within song types implies that Cozumel wrens demonstrate a form of preference. Similarly, male brown-throated wrens (*Troglodytes brunneicollis*) exhibit preference for specific syllables in their songs (Sosa-López & Mennill, 2014a).

Lapierre et al. (2011) found that more than half of the male song sparrows in their study showed song type preferences. Based on this finding they concluded that males were not efficiently displaying their repertoire size. The same can be said for male Adelaide's warblers during the dawn chorus (Petkau et al., 2025). The selective use of specific song types or syllables by Adelaide's warblers, rock wrens, Cozumel wrens, and brown-throated wrens suggests that different song types are not interchangeable (e.g., because they serve different functions) in these species.

4.1.2 Preferences are consistent across days

Males consistently preferred certain song types over others across recording days, even though the frequency of song use varied somewhat (Fig. 3.2, 3.3; Appendix 2, 3). The fact that males repeatedly use their preferred song types across recording days indicates a stable and consistent preference. Lapierre et al. (2011), in their study on the variation of use of locally common song elements in dawn singing of song sparrows (*Melospiza melodia*), reported that the degree to which males used highly shared song types was consistent within individuals during the nesting period across multiple days. This finding aligns with the consistency of song type preference in Adelaide's warbles across days.

4.1.3 Males prefer locally prevalent song types

The most important finding in this study is the strong positive relationship between individual preferences for certain song types during the dawn chorus and the local prevalence of those song types. This result suggests that males align their song type preferences with the local social norms of their neighbourhood (Table 3.4; Fig. 3.4). This behaviour may enhance communication for territory defense, reduce aggression, and attract mates. The observed preference for prevalent song types supports the general sharing hypothesis, which states that males preferentially sing highly shared songs at dawn (Lapierre et al., 2011), and is consistent with the social dynamics hypothesis, which states that birds communicate interactively at dawn to negotiate social relationships (Staicer et al., 1996).

This seems to be the first evidence in support of the general sharing hypothesis, as Lapierre et al. (2011) found no significant difference in the tendency for males to sing song types that have highly shared elements with their neighbours. Similarly, while rock wrens (*Salpinctes obsoletus*) also exhibit individual song type preferences, Benedict and Warning (2017) reported that these preferences were not driven by consistent patterns of song use within their population. The closest findings that support males modifying their singing pattern in response to the prevalent song type within their breeding population was recorded in nocturnal singing of nightingales. Kiefer et al. (2010) found that young nightingales retained commonly sung song types in their second breeding season while eliminating rare songs (a type of selective attrition), leading to greater conformity within the population over time.

Birds may prefer locally prevalent song types because they are useful for a form of vocal interaction known as countersinging. For example, male banded wrens (*Thryothorus pleurostictus*) prefer to use shared song types with neighbours during countersinging (Trillo & Vehrencamp, 2005). As a form of territory defense or social interaction, males of many songbirds engage in countersinging (Logue, 2021), during which one male may respond to another's song with the same song type ("song type matching") or another song that they both share ("repertoire matching"). Species like the song sparrows *(Melospiza melodia*; Beecher, 1996), black-capped chickadees (*Poecile atricapillus*; Fitzsimmons et al., 2008), field sparrows (*Spizella pusilla*; Nelson & Croner, 1991), and chestnut-sided warblers *(Setophaga pensylvanica*; Byers, 1995) provide strong evidence that males selectively match neighbours' songs. The persistent use of shared songs during interactions indicates that countersinging behaviours likely influence song type preference.

4.1.4 Males prefer song types with some superior transmission properties

I predicted that if males prefer song types with superior transmission properties, they would favour song types with low mean frequency, low percent sound, high amplitude, and high vocal deviation (Table 3.1). While males preferred song types with low frequency and low percent sound, they did not show a preference for high amplitude (i.e., songs that are loud) or high vocal deviation (Table 3.3). This is similar to the findings of Benedict and Warning (2017), which showed that rock wrens (*Salpinctes obsoletus*) prefer song types that enhance long-distance signal transmission. The preferred song types were characterized by longer durations, lower frequencies, narrower bandwidths, and slower syllable trill rates. Like rock wrens, male Adelaide's warblers appear to prefer song types with low frequency, which propagate more efficiently in their environment, supporting the idea that transmission properties influence song selection.

The dawn chorus is a critical period for male songbirds to broadcast their songs over long distances, making transmission efficiency particularly important. Atmospheric conditions before sunrise, characterized by lower temperatures, reduced wind, and minimal air turbulence, enhance sound propagation (Dabelsteen & Mathevon, 2002; Henwood & Fabrick, 1979). These factors allow songs to travel farther with less degradation, increasing their effectiveness in territory defense and mate attraction. Given these acoustic advantages, selection may favour song structures that optimize transmission, making certain song types more prevalent during dawn singing. This idea aligns with the Acoustic Adaptation Hypothesis (AAH), which suggests that acoustic signals evolve to maximize their transmission efficiency within specific environments (Morton, 1975). By preferring song types with lower frequencies that are less attenuated, male Adelaide's warblers may be adjusting their songs to take advantage of the sound propagation conditions during the dawn chorus.

4.1.5 Males do not prefer song types with high vocal performance but may prefer song types with low performance

Males preferred song types with low percent sound, but their preferences were not influenced by amplitude or vocal deviation. These findings do not support the hypothesis that they prefer song types that require high vocal performance (Table 3.1; 3.3). The findings are, however, somewhat consistent with the hypothesis that they prefer song types with low performance requirements. High performance songs are energetically costly (Podos, 1997) and may only be worth singing when sufficiently motivated, such as during aggressive encounters or when attracting mates (Logue et al., 2020). This could mean that males prefer less demanding (low performance) song types at dawn because they are not motivated enough to challenge the limits of performance at that time, instead prioritizing ease of production and energy conservation. Cardoso and Atwell (2016) found that song types shared among male dark-eyed juncos (*Junco hyemalis*) exhibited low performance levels compared to unshared song types. This finding perfectly aligns with my findings that preferred song types in male Adelaide’s warblers tend to be both widely shared and low performance.

4.2 Broader Implications

The overall findings suggest that male Adelaide's warblers balance multiple factors in their song type preferences during the dawn chorus. Social context seems to play a significant role, emphasizing the importance of communication within social networks. The consistent preferences observed across different days highlight the reliability of individual signalling strategies.

4.3 Future direction

Further research could explore patterns of within-individual song type variation across years to gain preference insights into whether preferences remain stable or change as a result of age, experience, environmental changes, or social interactions. Another significant area of research would be to assess the stability of individual song type preference during daytime singing, as well as exploring the extent to which acoustic transmission properties and vocal performance similarly influence preference outside of the dawn chorus. Finally, understanding how males use their shared and unshared song types during the dawn chorus will provide clues about the value of singing prevalent song types.

4.4 Conclusion

This study presents strong evidence regarding song type preferences in male Adelaide’s warblers, emphasizing the significance of individual consistency and social dynamics. Although the functional acoustic properties and vocal performance were less influential, the preference for shared song types highlights the importance of local communication networks in influencing male song behaviour.

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APPENDIX 1: Histograms showing the distribution of song type preference in individual males with the red broken lines representing uniform distribution.

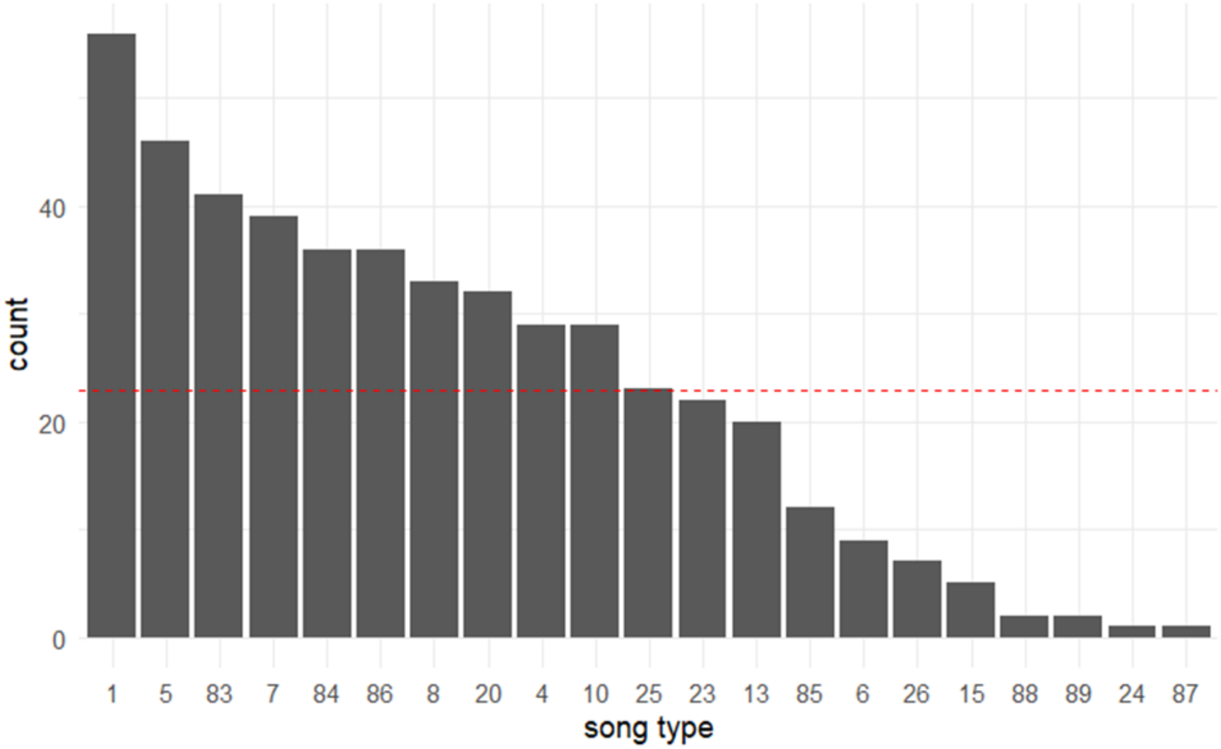

Figure 1: A histogram showing the distribution of song types recorded from male WLpTb. The red broken lines represent the expectation under a uniform distribution.

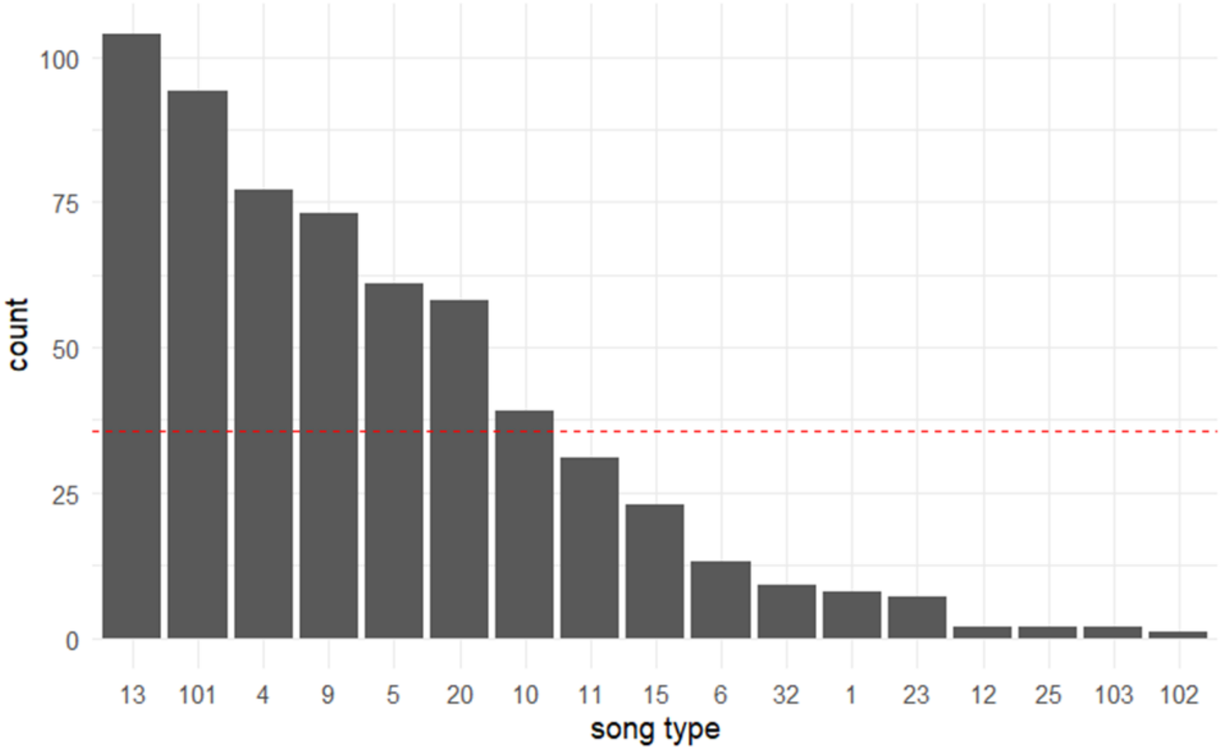

Figure 2: A histogram showing the distribution of song types recorded from male TbWY. The red broken lines represent the expectation under a uniform distribution.

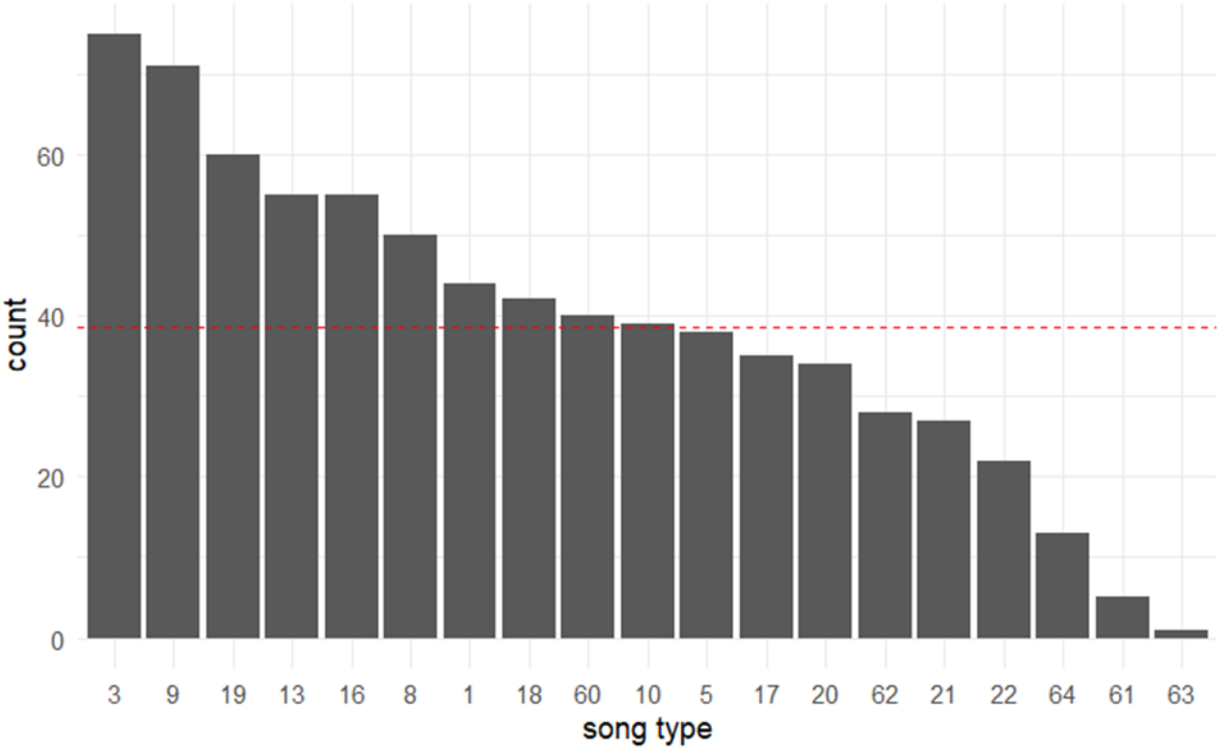

Figure 3: A histogram showing the distribution of song types recorded from male TbTbLg. The red broken lines represent the expectation under a uniform distribution.

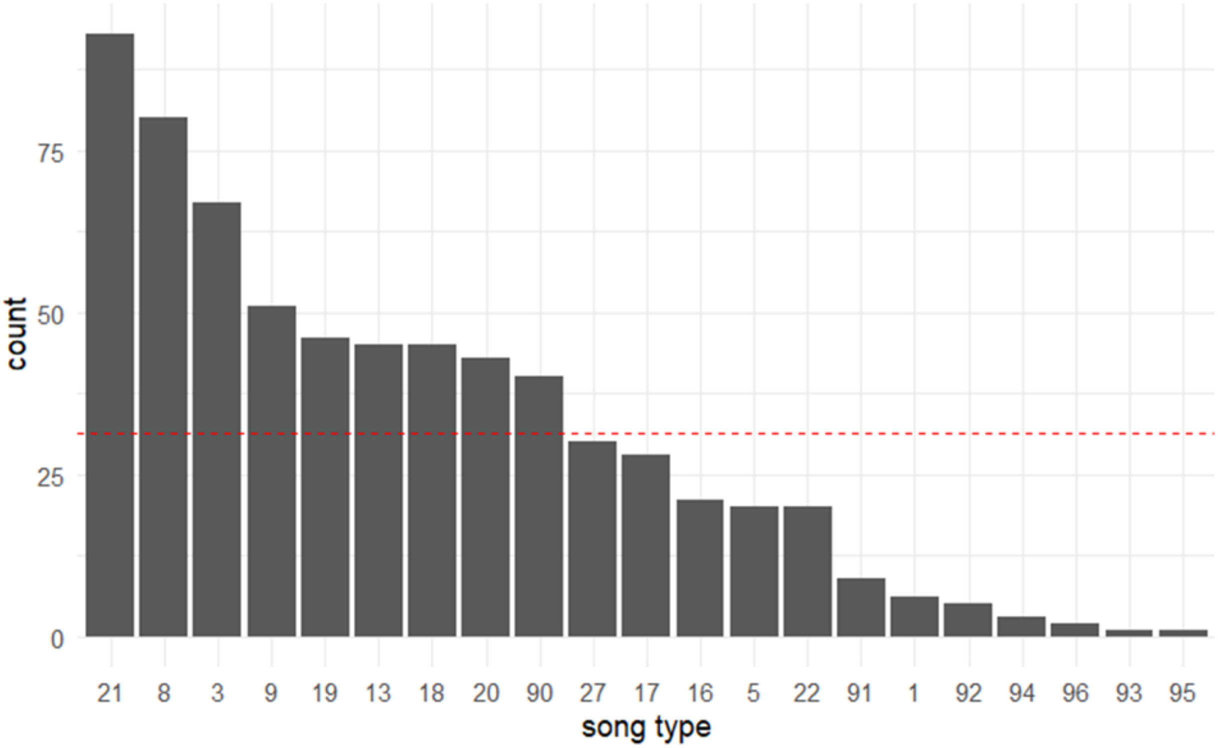

Figure 4: A histogram showing the distribution of song types recorded from male RbDgY. The red broken lines represent the expectation under a uniform distribution.

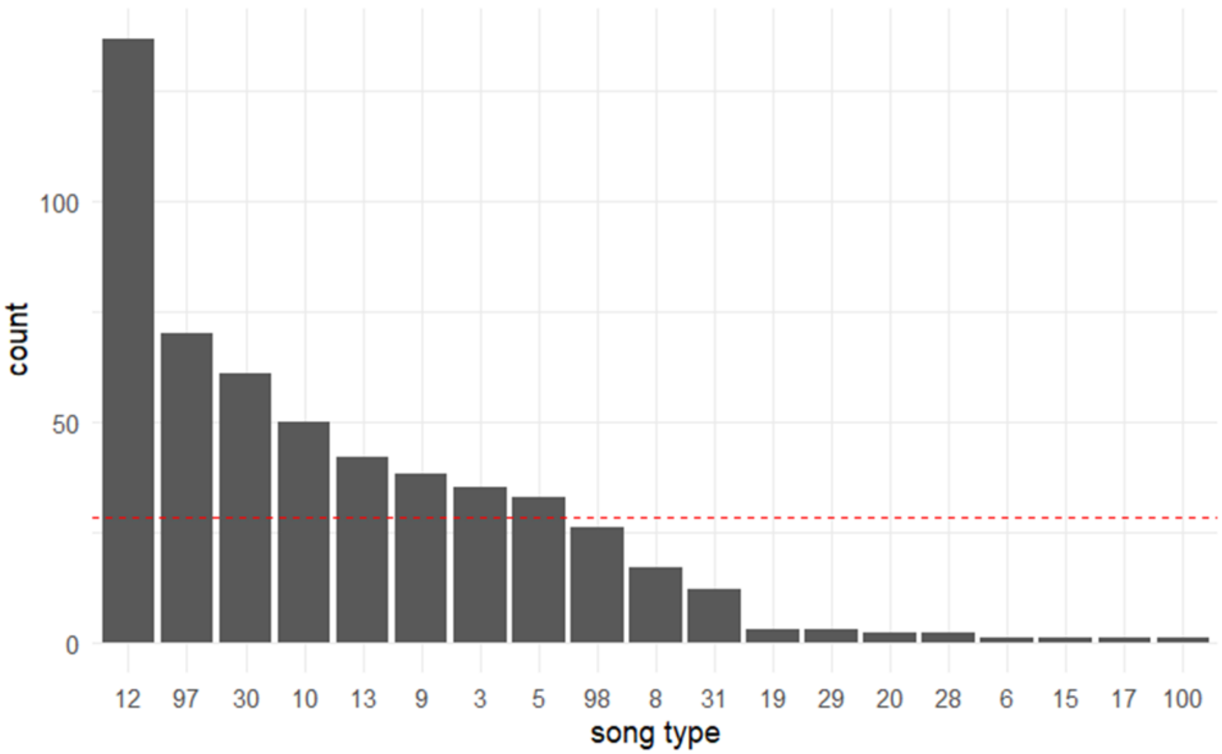

Figure 5: A histogram showing the distribution of song types recorded from male RRO. The red broken lines represent the expectation under a uniform distribution.

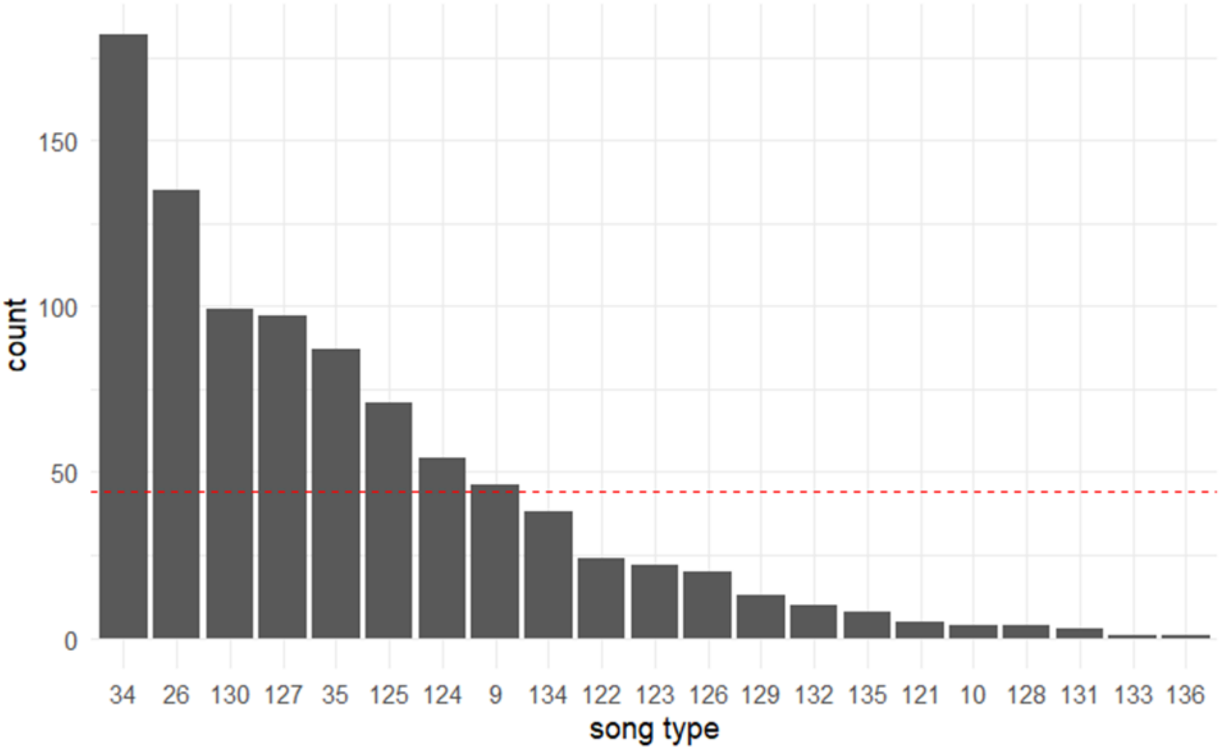

Figure 6: A histogram showing the distribution of song types recorded from male OPR. The red broken lines represent the expectation under a uniform distribution.

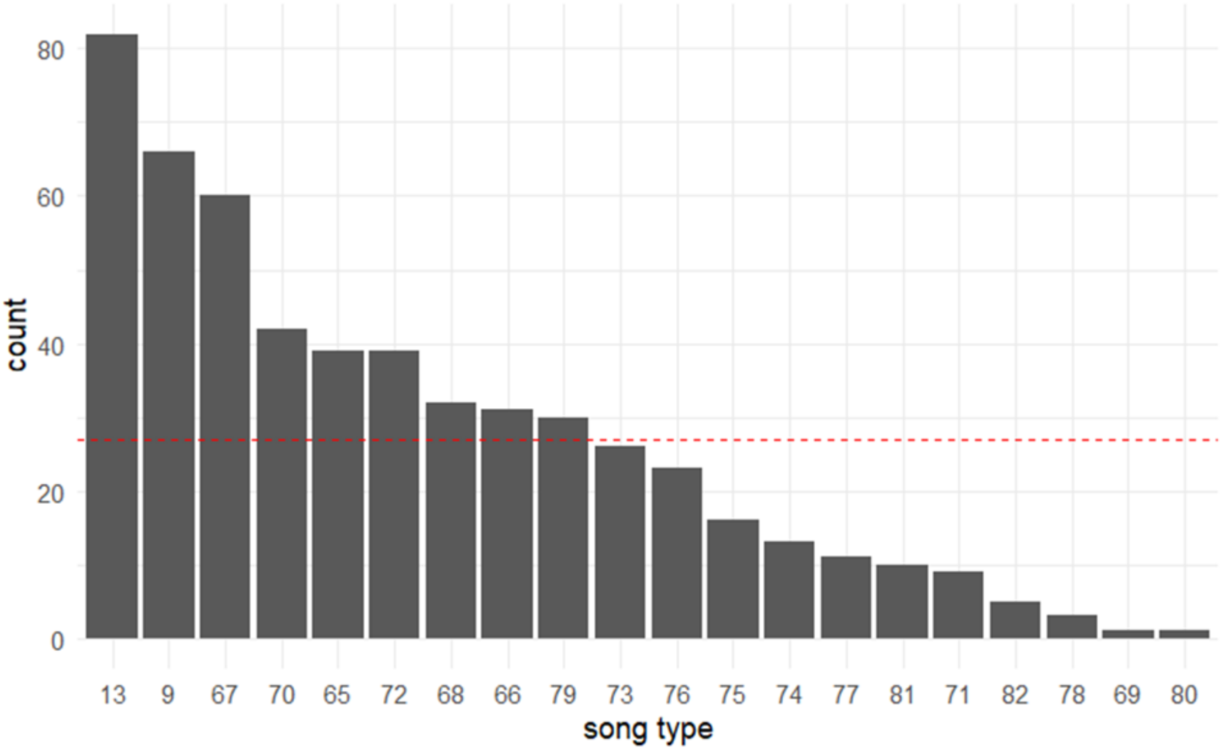

Figure 7: A histogram showing the distribution of song types recorded from male LpRbTb. The red broken lines represent the expectation under a uniform distribution.

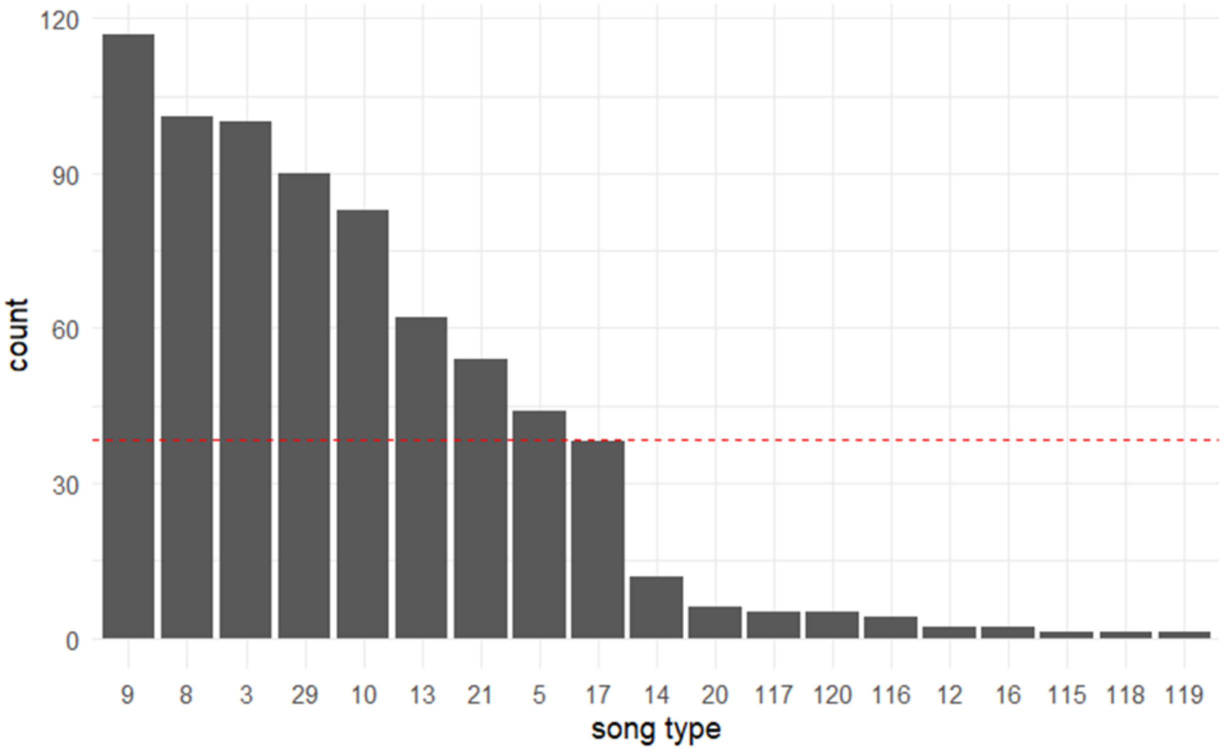

Figure 8: A histogram showing the distribution of song types recorded from male LbOW. The red broken lines represent the expectation under a uniform distribution.

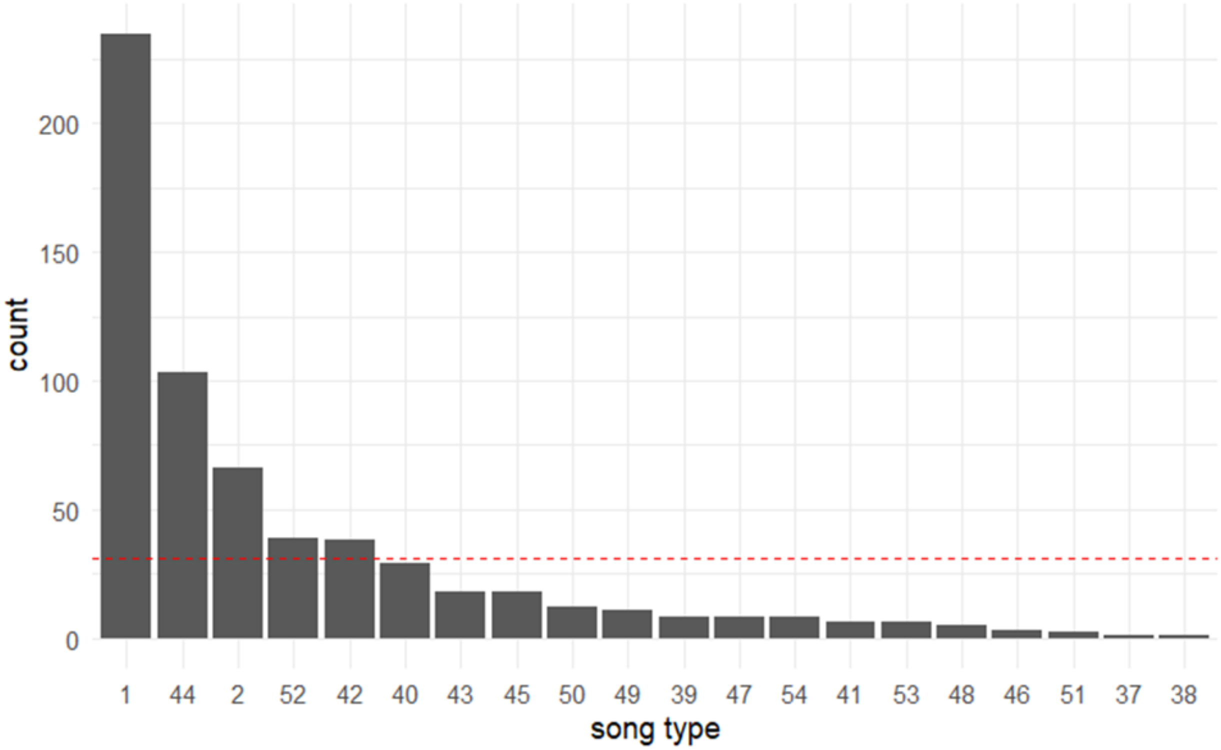

Figure 9: A histogram showing the distribution of song types recorded from male LbLpY. The red broken lines represent the expectation under a uniform distribution.

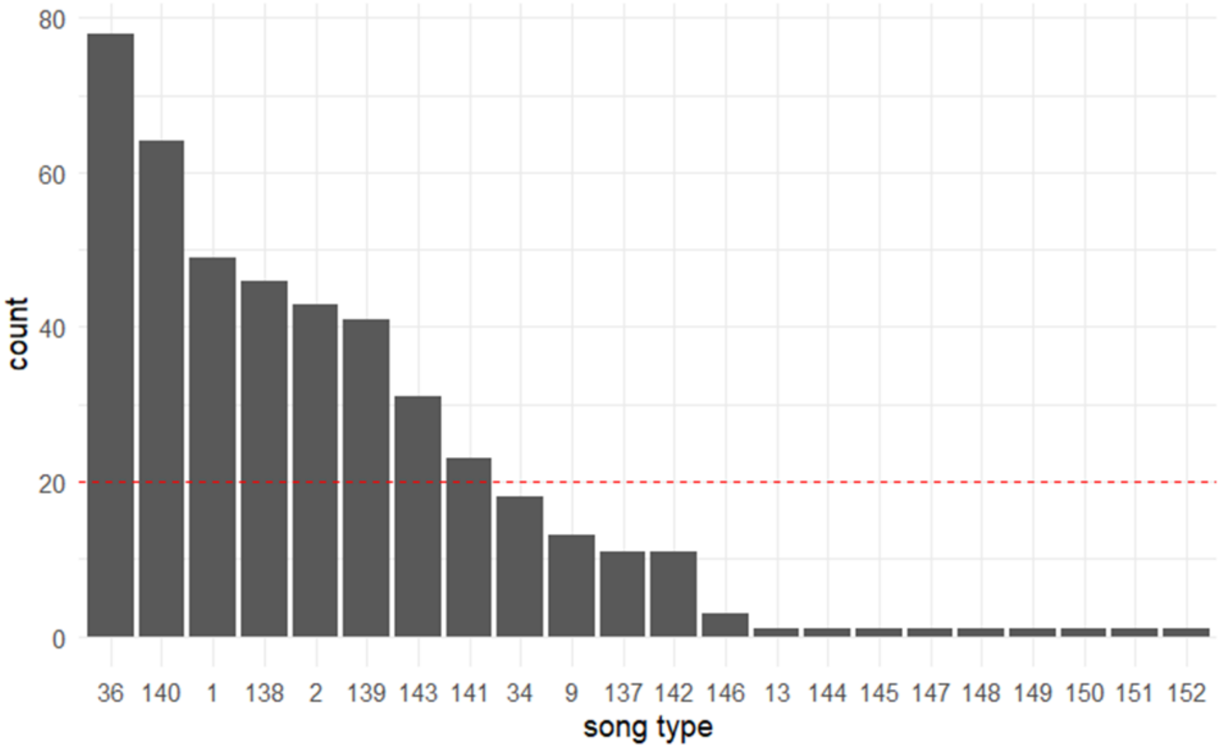

Figure 10: A histogram showing the distribution of song types recorded from male KWY. The red broken lines represent the expectation under a uniform distribution.

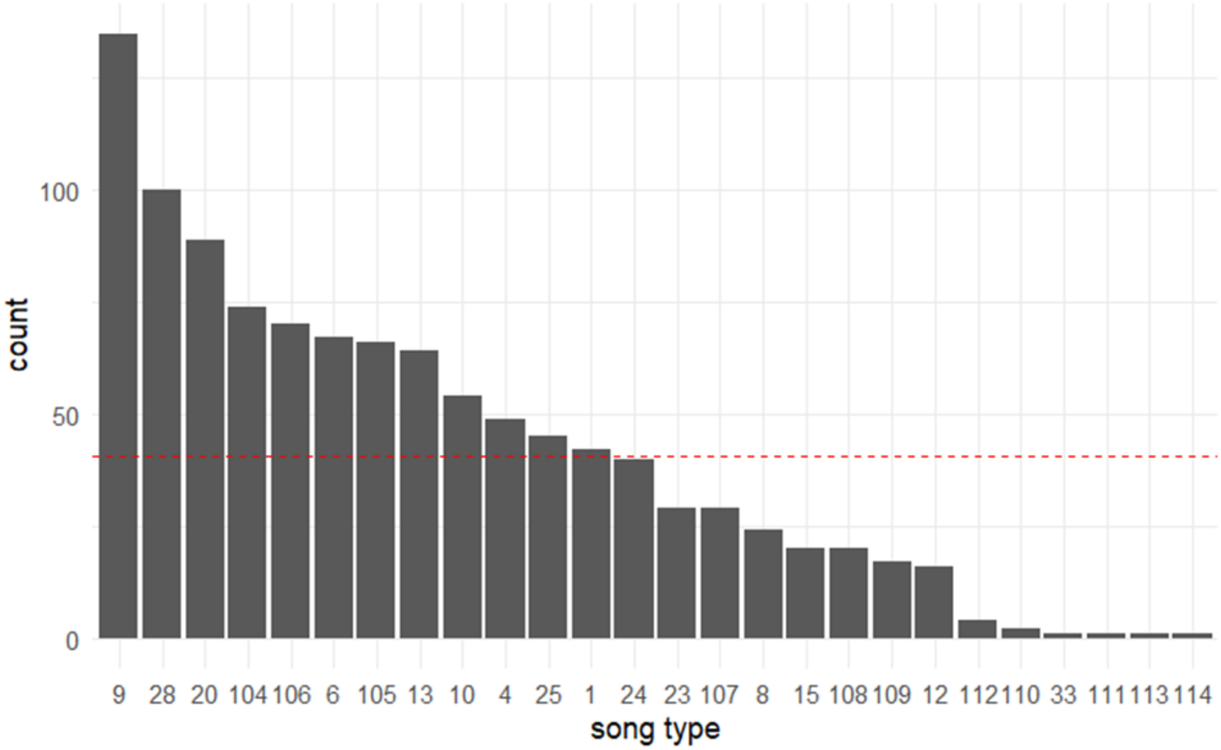

Figure 11: A histogram showing the distribution of song types recorded from male KRDg. The red broken lines represent the expectation under a uniform distribution.

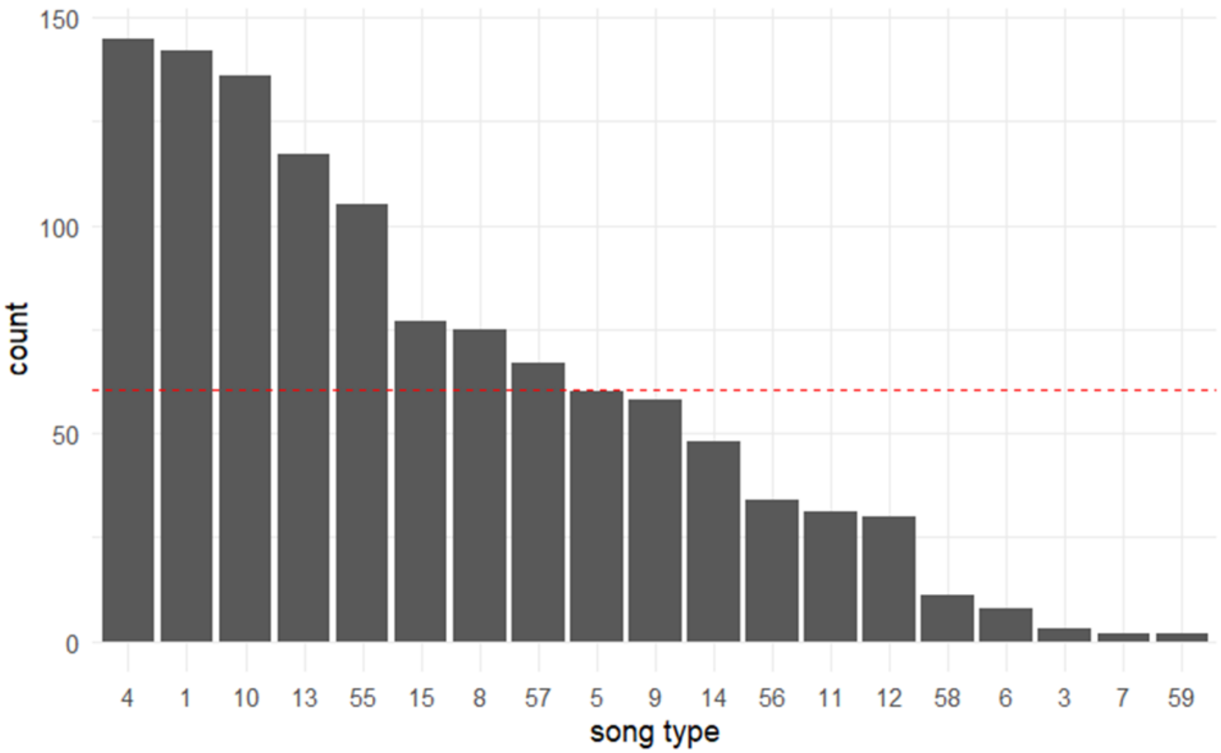

Figure 12: A histogram showing the distribution of song types recorded from male KLgK. The red broken lines represent the expectation under a uniform distribution.

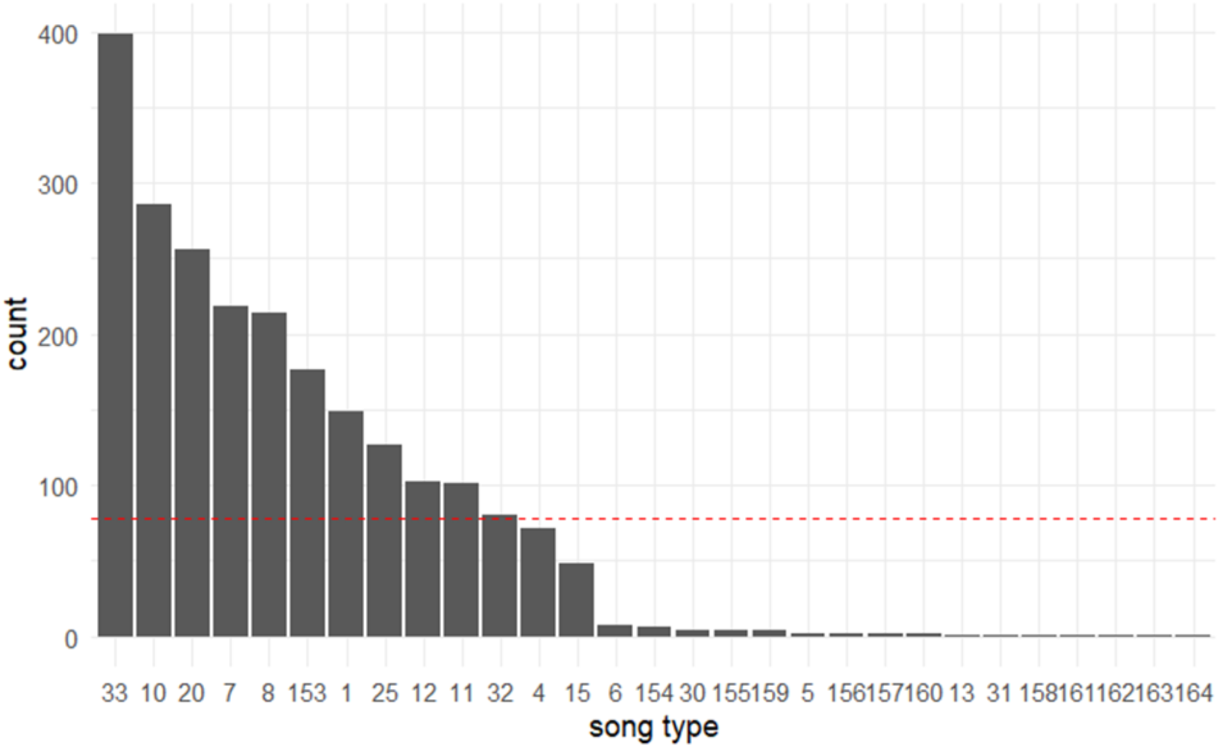

Figure 13: A histogram showing the distribution of song types recorded from male DgTbO. The red broken lines represent the expectation under a uniform distribution.

APPENDIX 2: Full model results of consistent individual preference across days.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	3.19	0.26	2.66	3.67	1.01	356	861
num_neighbours_s	0.83	0.23	0.38	1.31	1.01	384	880
avg_mean_freq_s	-0.46	0.03	-0.53	-0.40	1.00	2907	4551
avg_percent_sound_s	-0.23	0.03	-0.29	-0.17	1.00	4037	5346
avg_rms_s	0.01	0.06	-0.11	0.13	1.00	2857	4580
avg_consensus_dev_s	-0.02	0.04	-0.09	0.05	1.00	2418	3997

APPENDIX 3: Forest plots of song type use for individual males with each point representing the estimate of count for each song type and the horizontal lines showing 95% confidence intervals.

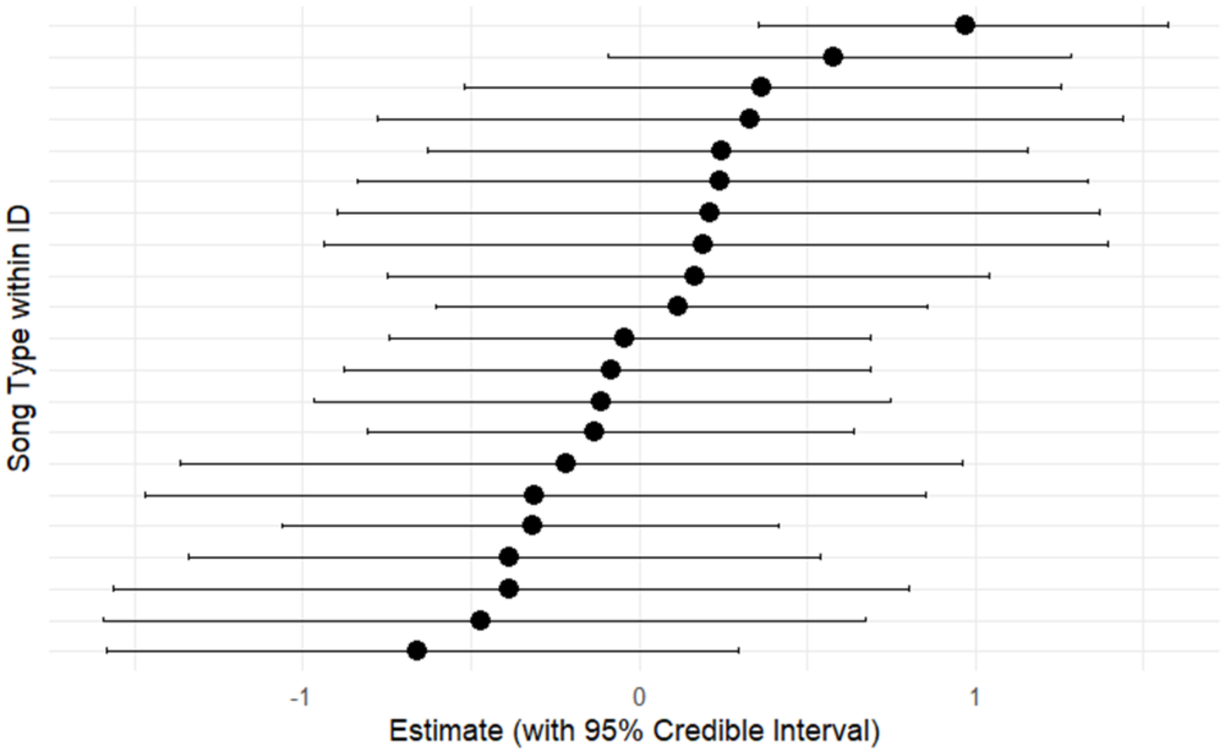

Figure 1: A forest plot of song type use for male WLpTb. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

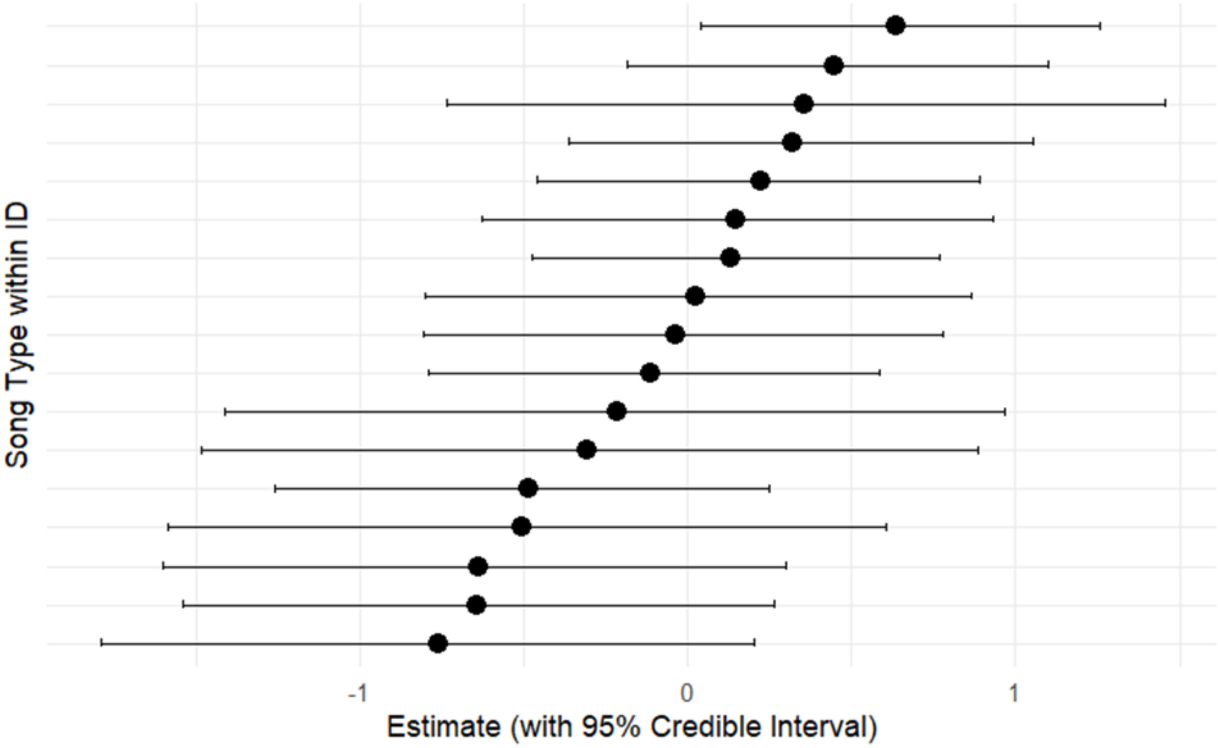

Figure 2: A forest plot of song type use for male TbWY. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

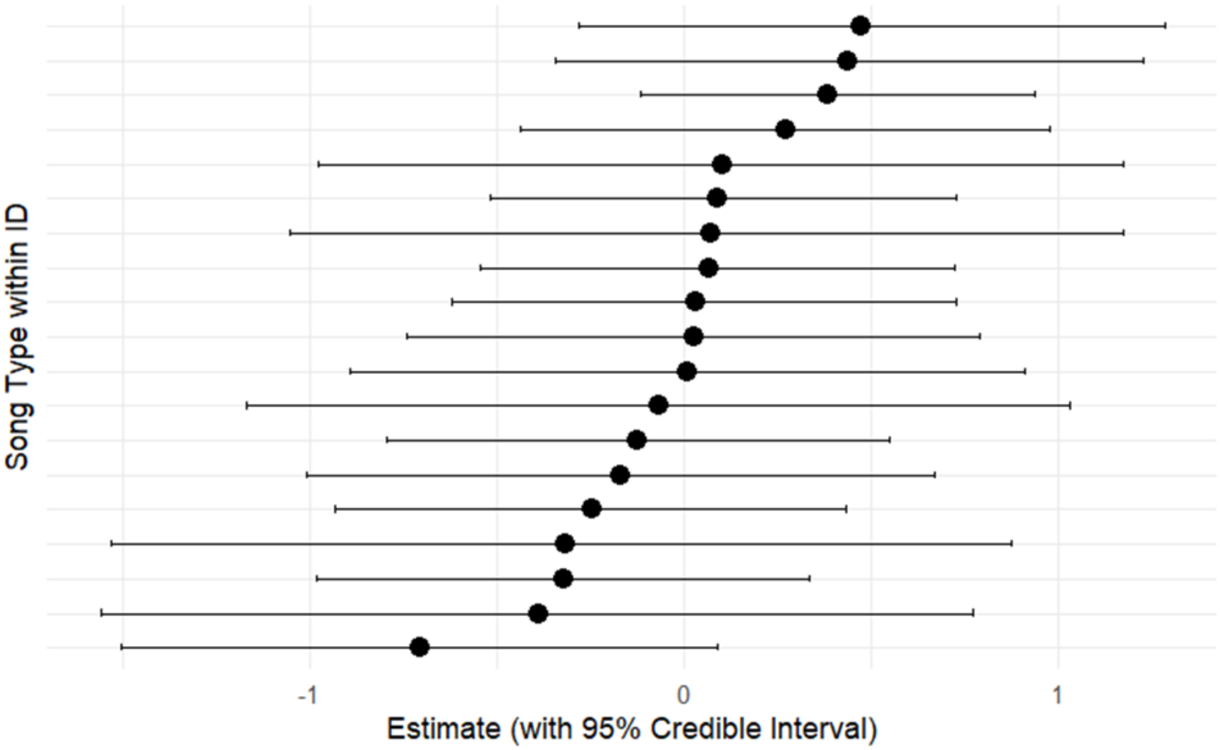

Figure 3: A forest plot of song type use for male TbTbLg. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

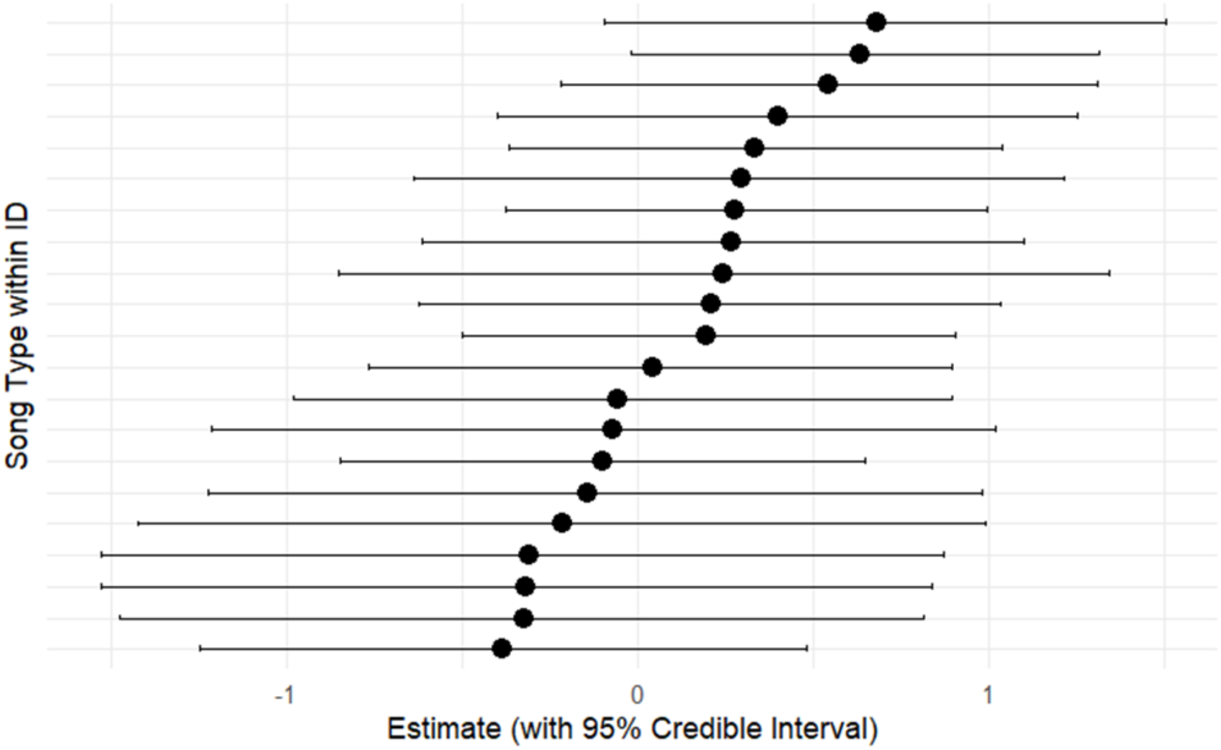

Figure 4: A forest plot of song type use for male RbDgY. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

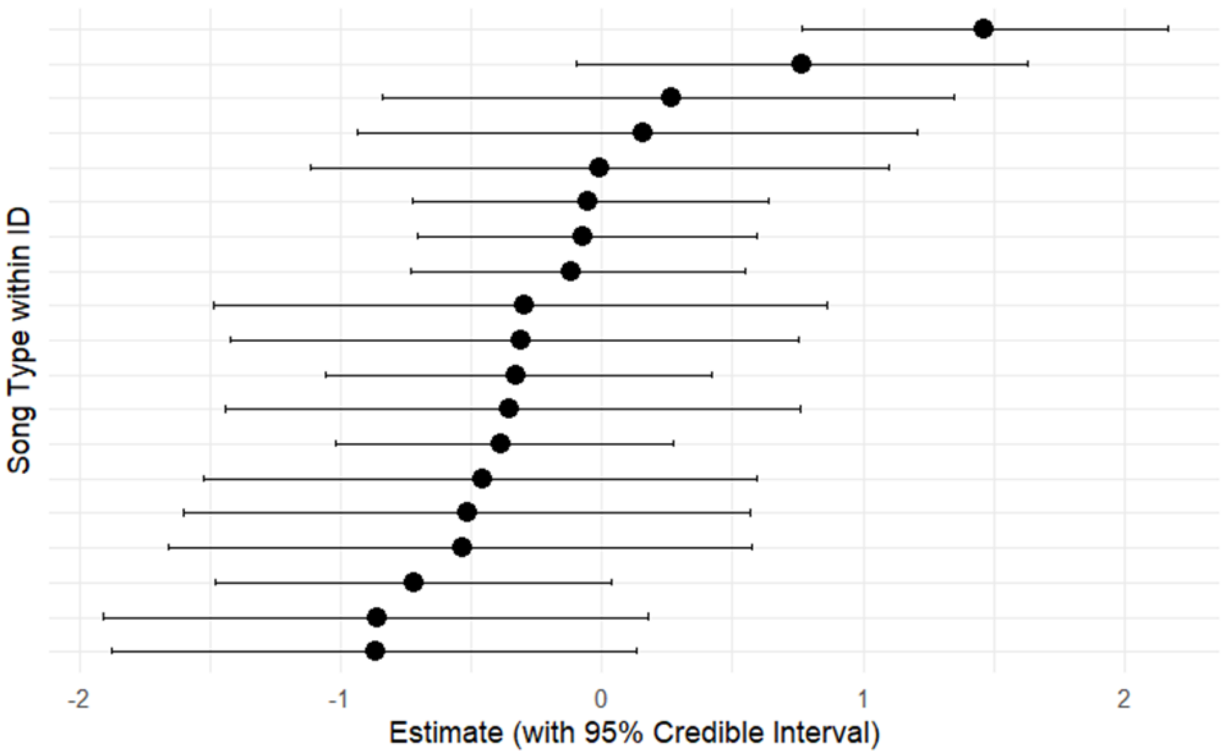

Figure 5: A forest plot of song type use for male RRO. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

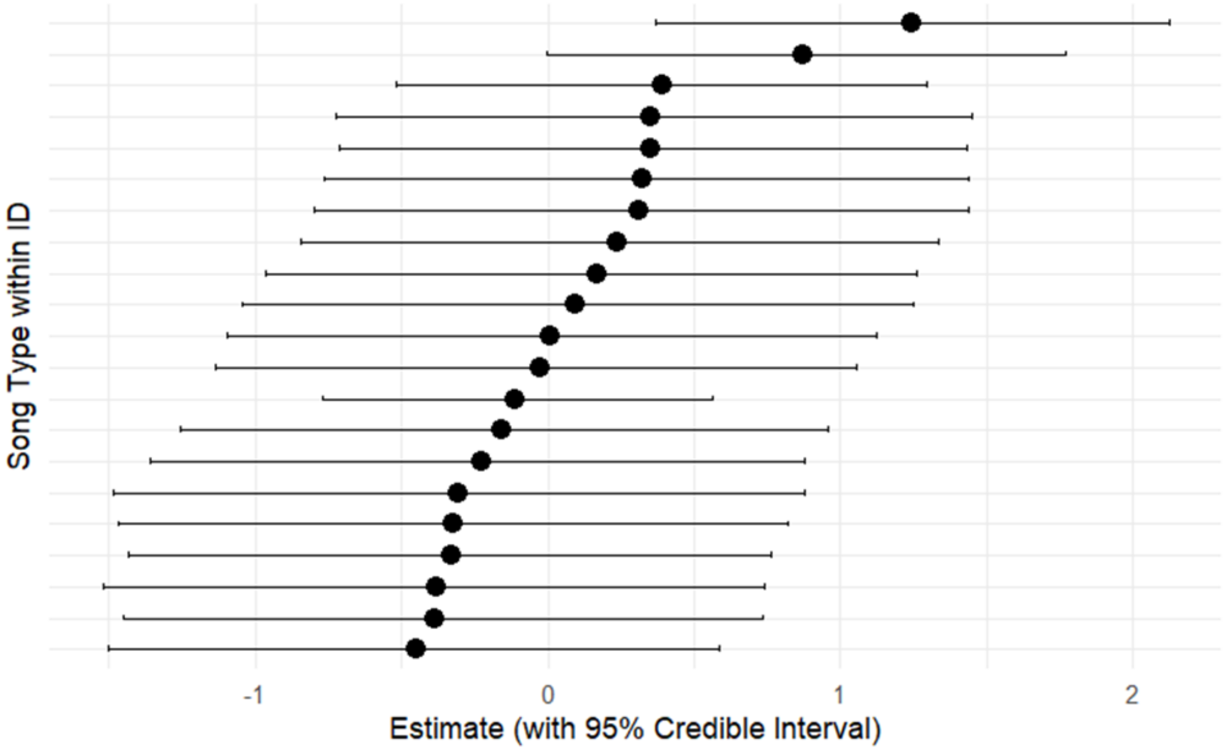

Figure 6: A forest plot of song type use for male OPR. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

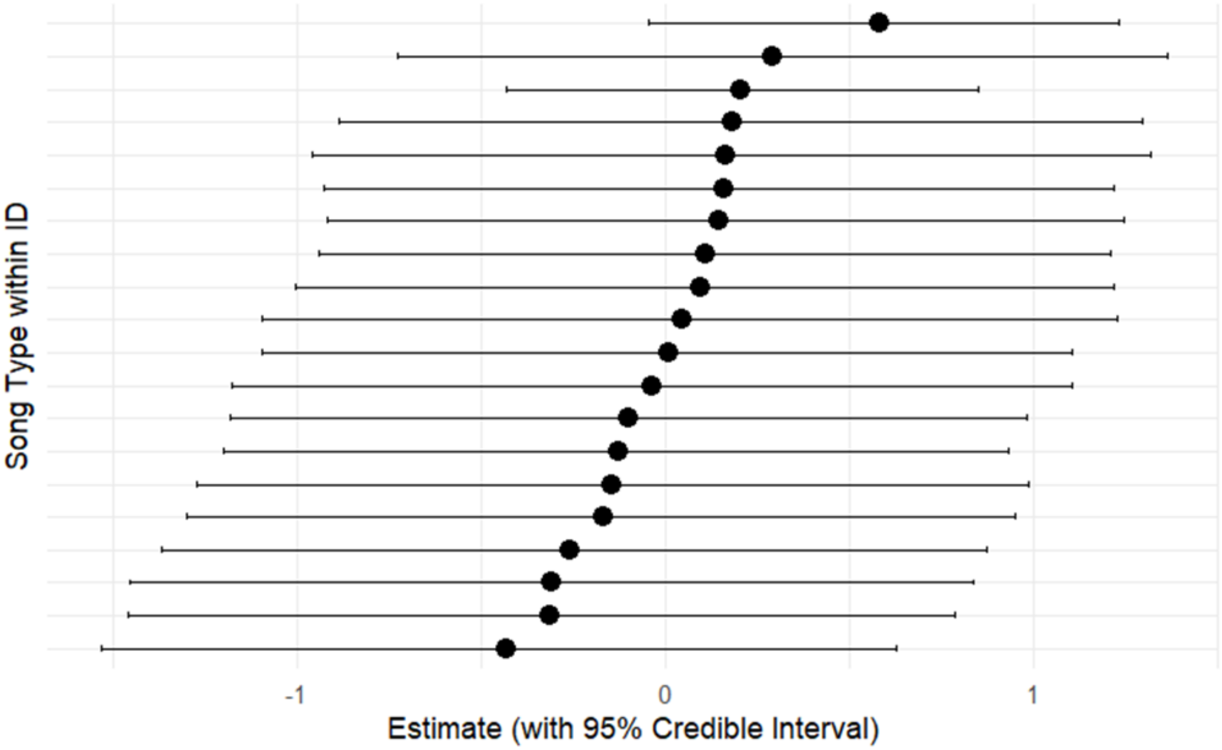

Figure 7: A forest plot of song type use for male LpRbTb. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

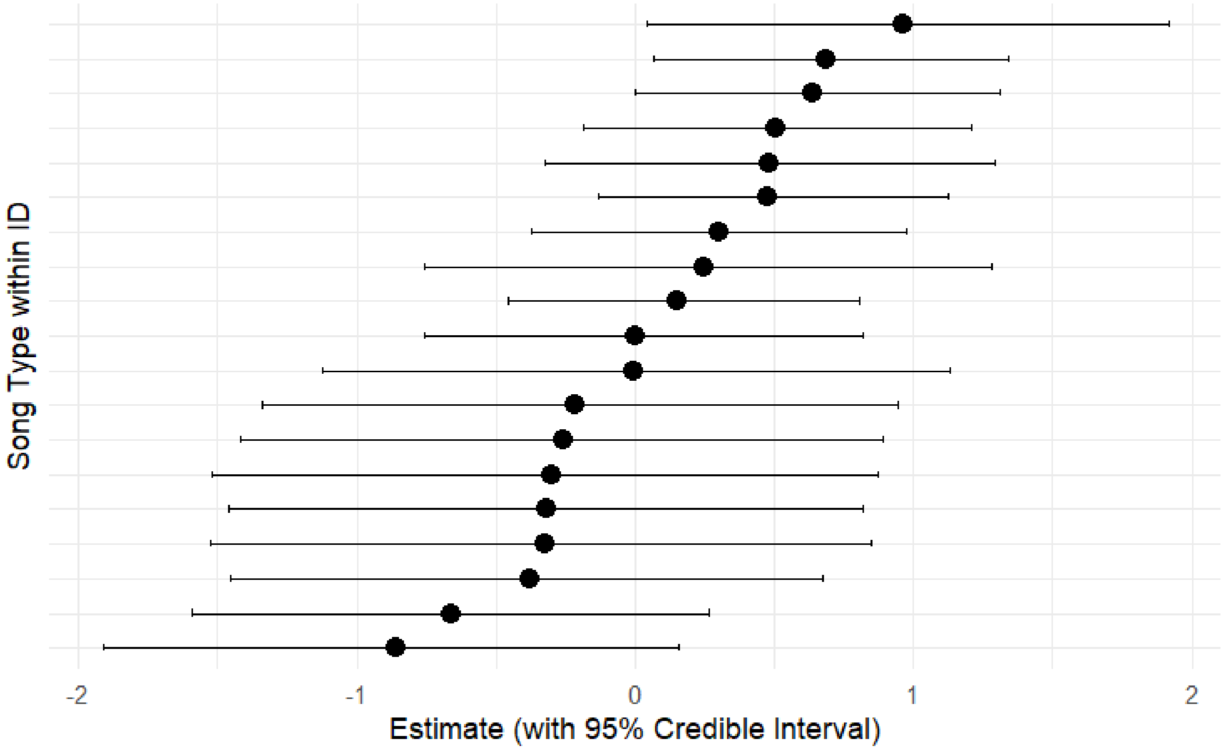

Figure 8: A forest plot of song type use for male LbOW. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

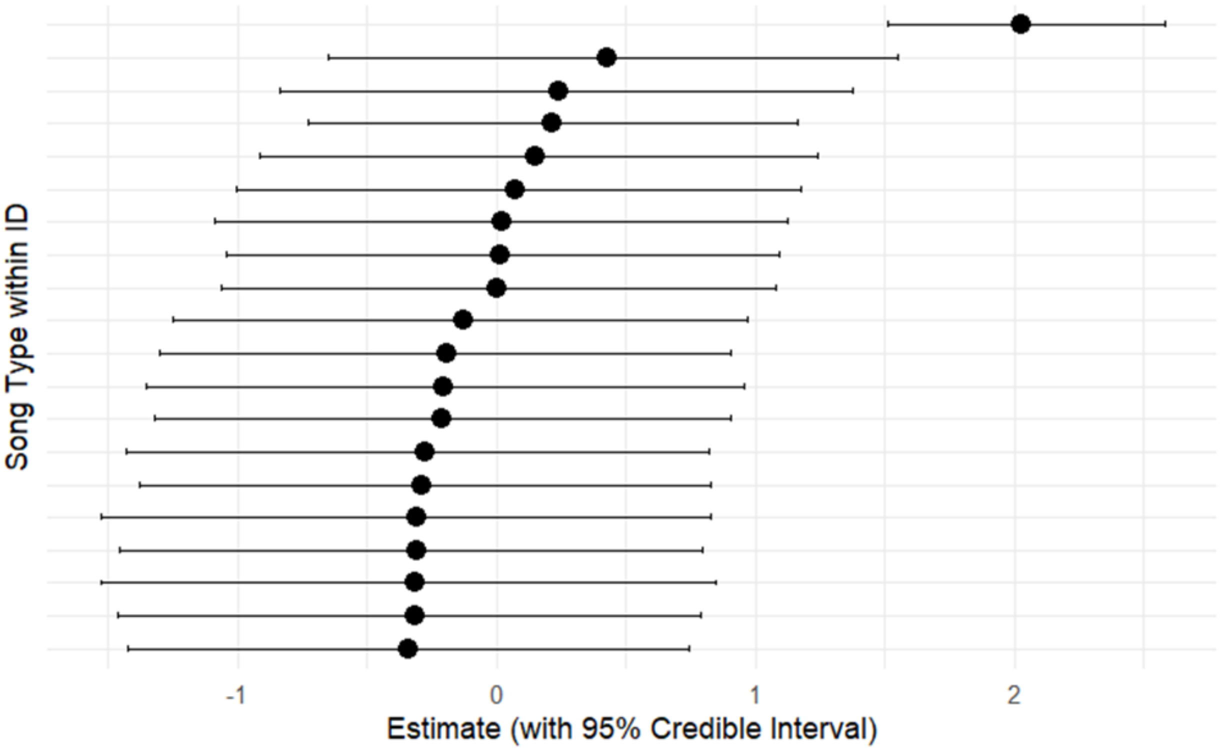

Figure 9: A forest plot of song type use for male LbLpY. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

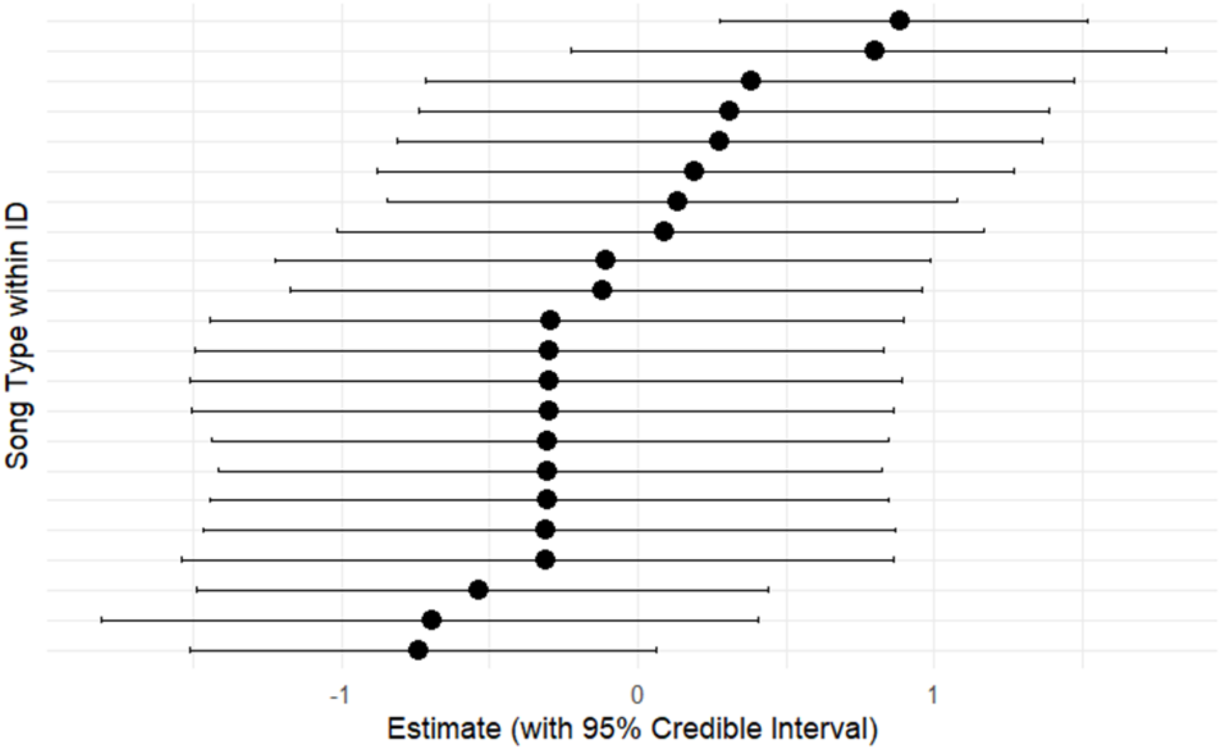

Figure 10: A forest plot of song type use for male KWY. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

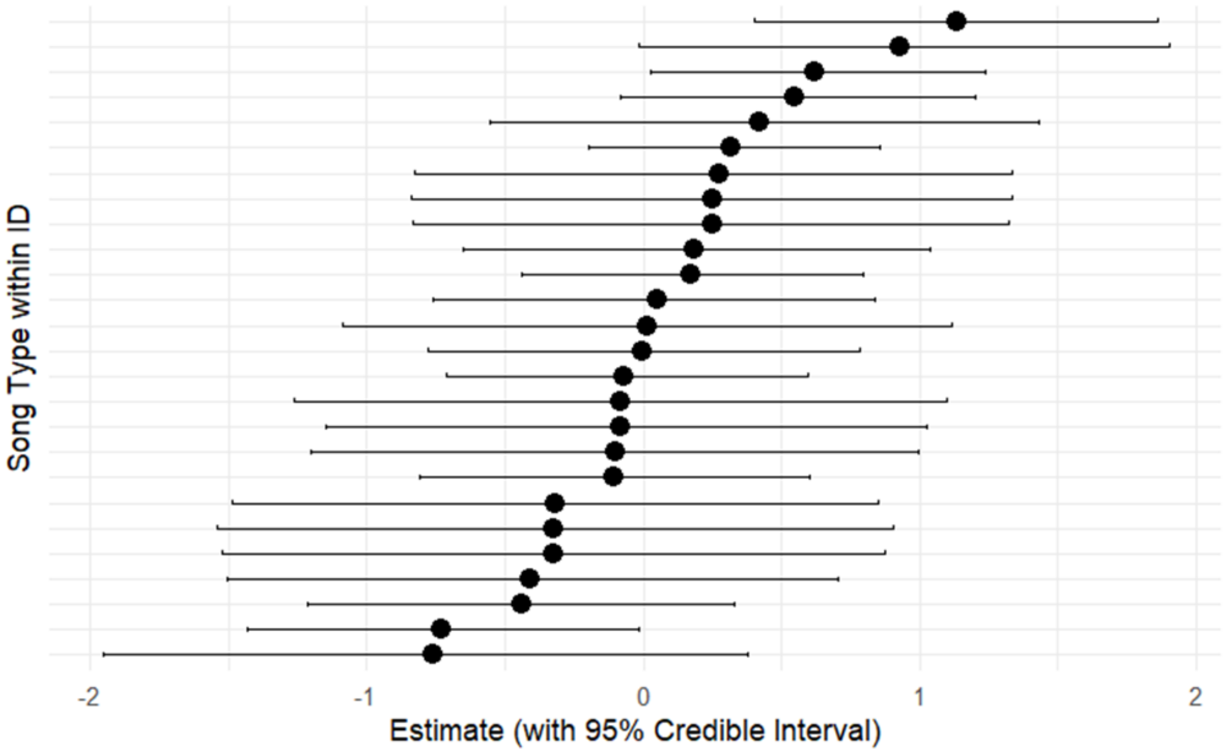

Figure 11: A forest plot of song type use for male KRDg. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

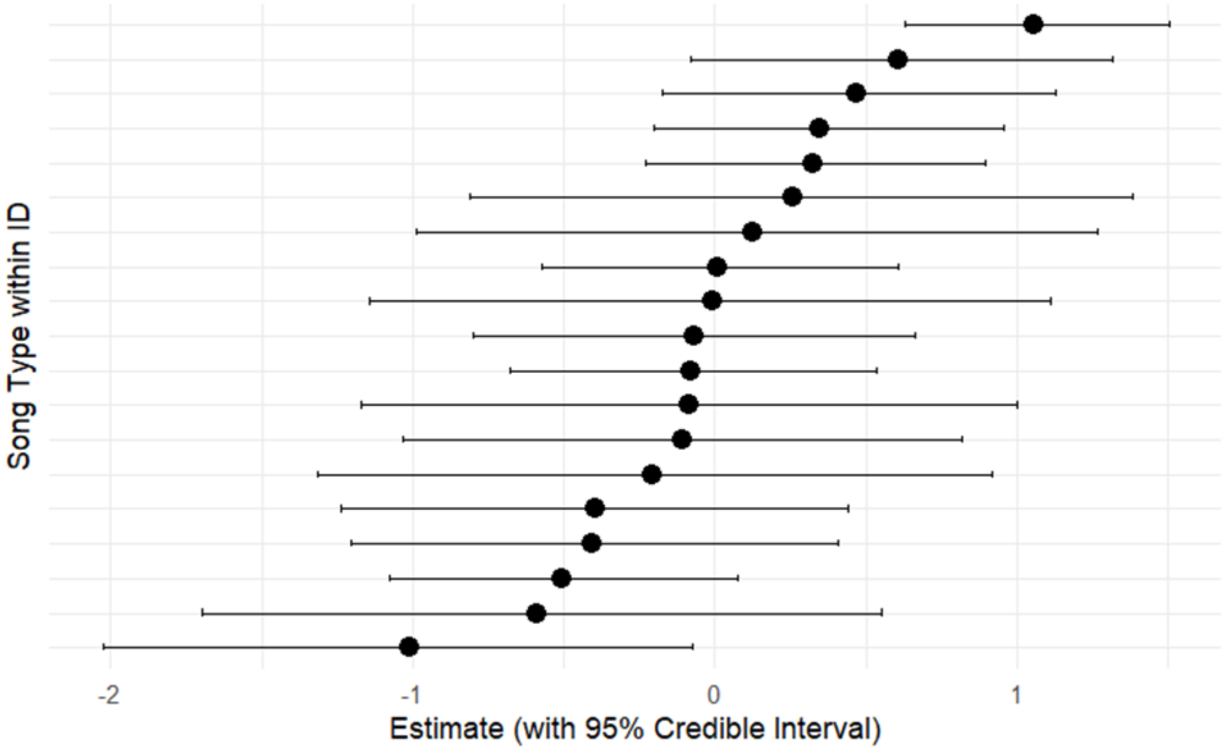

Figure 12: A forest plot of song type use for male KLgK. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

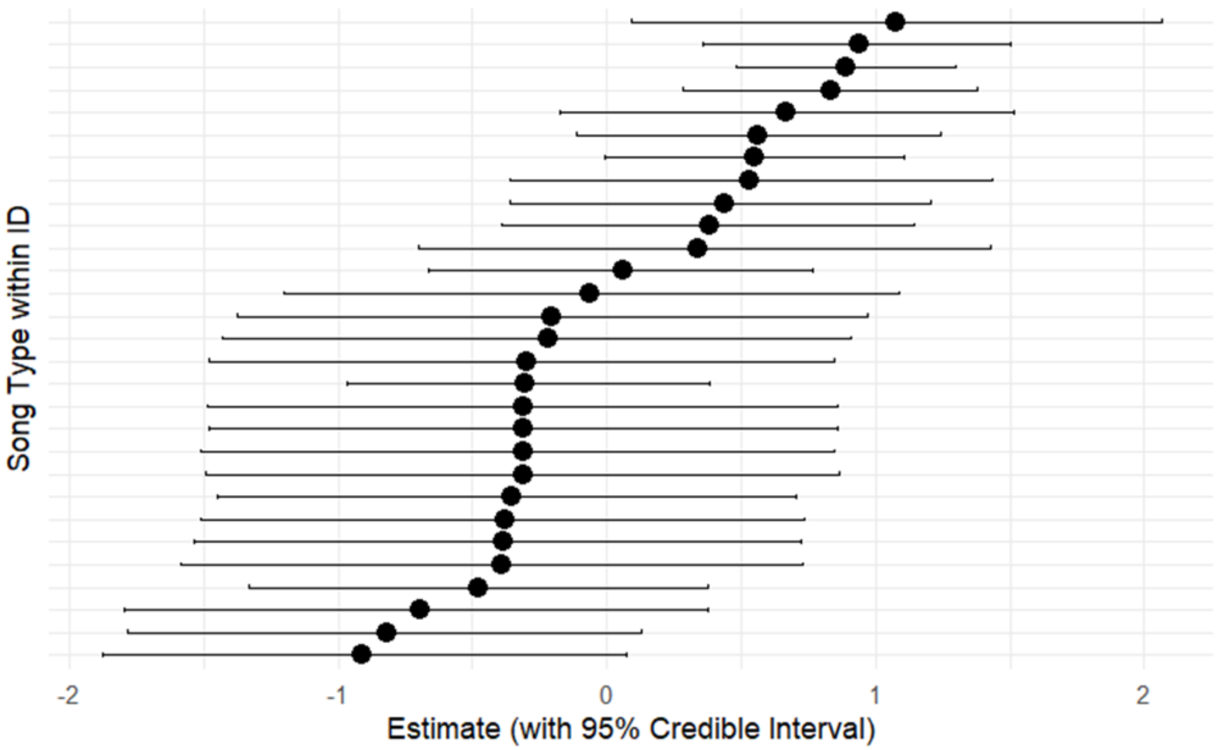

Figure 13: A forest plot of song type use for male DgTbO. Points represent the estimate of the count for each song type sung by each male in our sample. Horizontal lines show 95% confidence intervals.

APPENDIX 4: Line graphs showing the count of each male's nine randomly selected song types over days. Each colour represents a different song type.

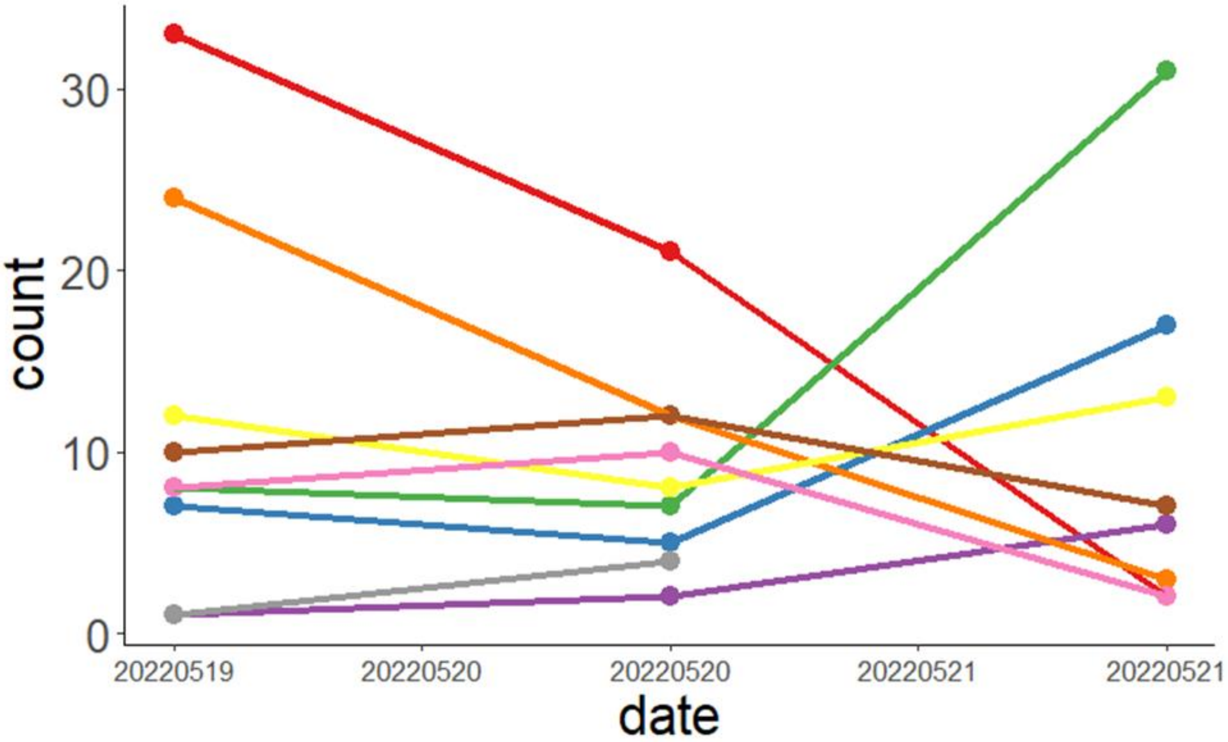

Figure 1: A line graph showing the count of nine of male WLpTb's song types over six days. Each colour represents a different song type.

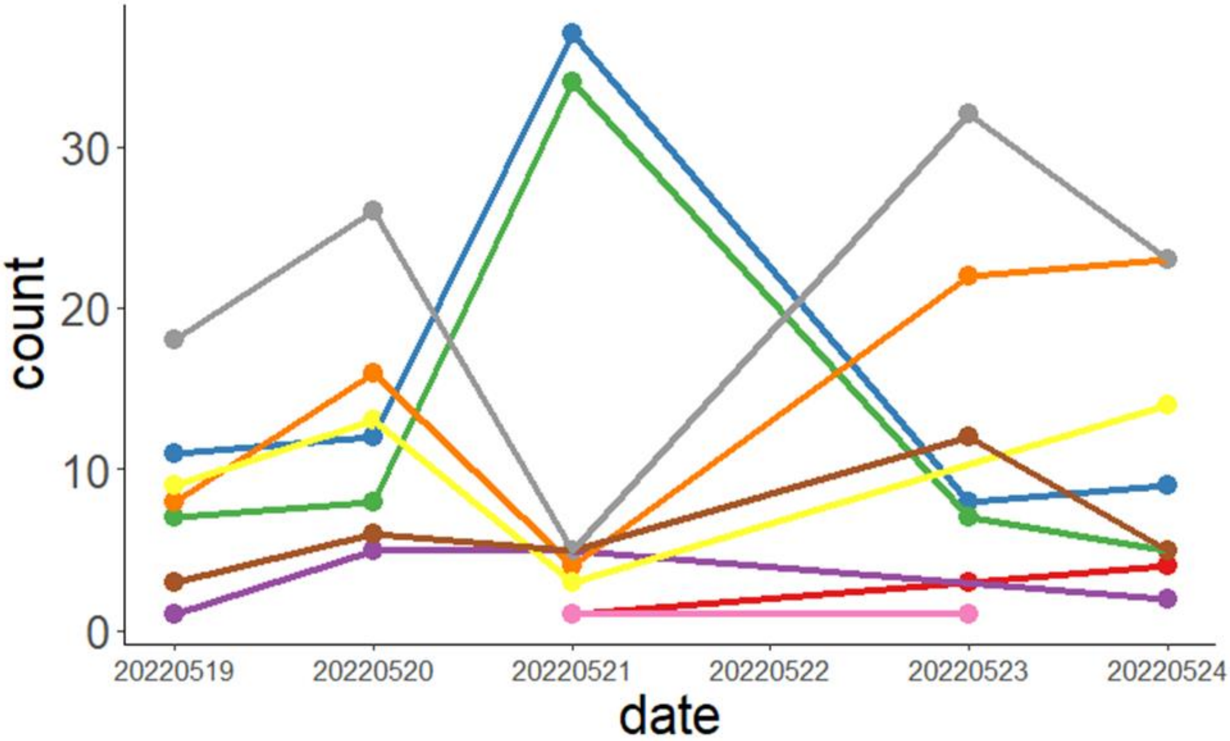

Figure 2: A line graph showing the count of nine of male TbWY's song types over six days. Each colour represents a different song type.

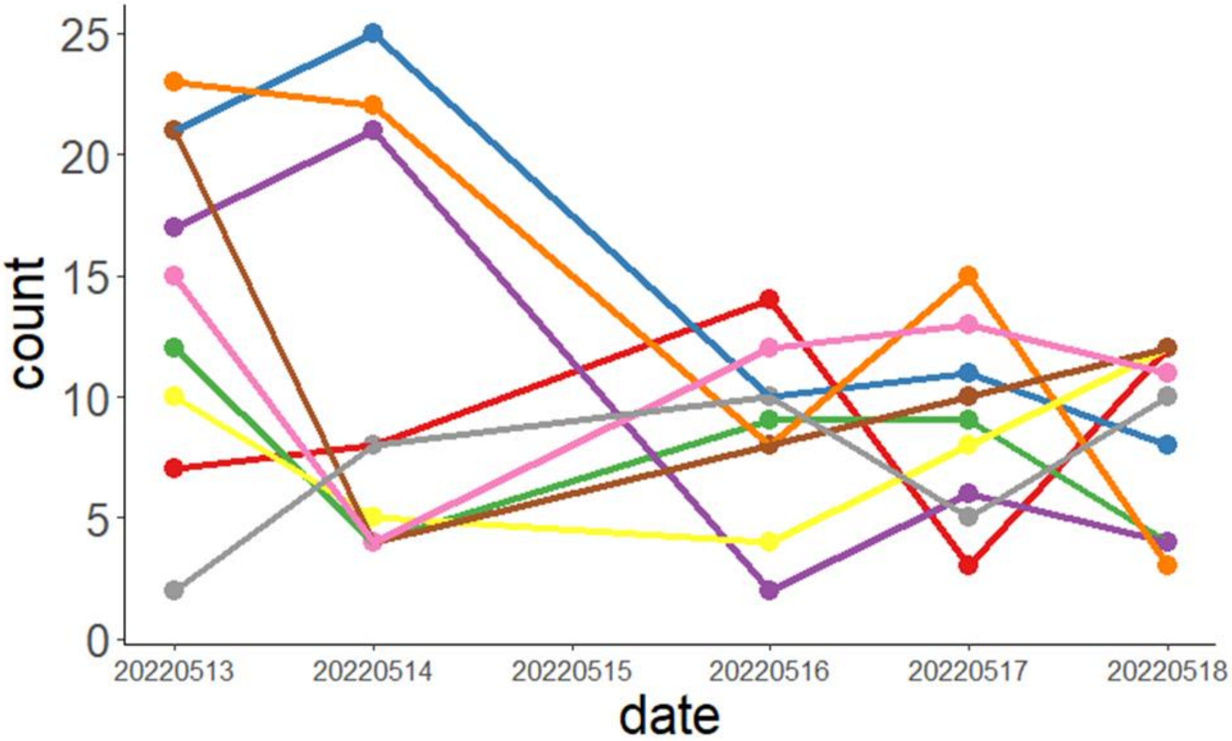

Figure 3: A line graph showing the count of nine of male TbTbLg's song types over six days. Each colour represents a different song type.

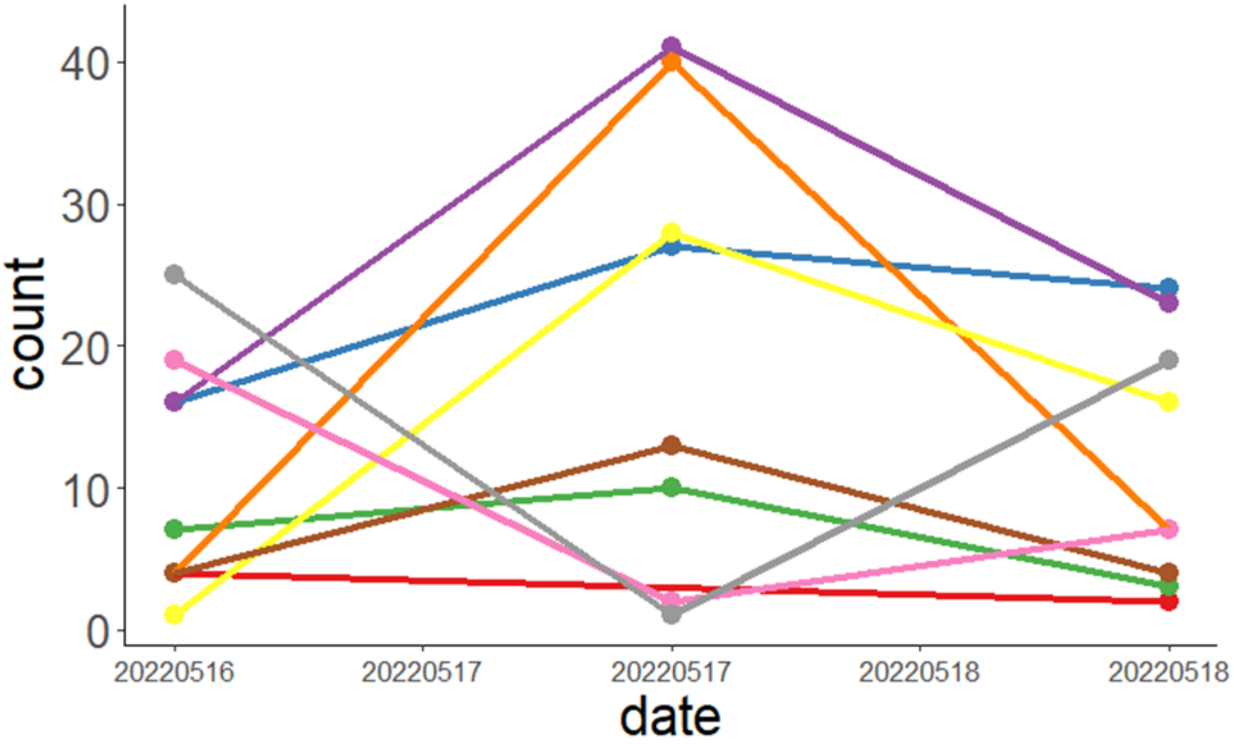

Figure 4: A line graph showing the count of nine of male RbDgY's song types over six days. Each colour represents a different song type.

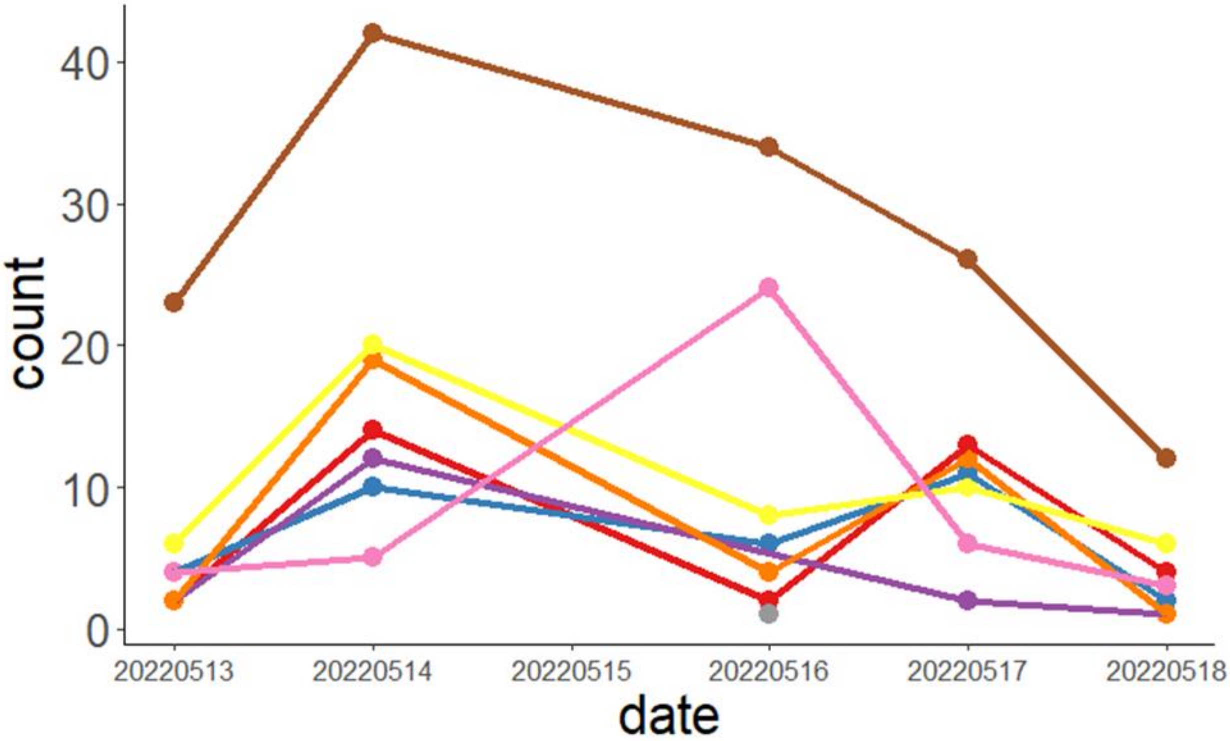

Figure 5: A line graph showing the count of nine of male RRO's song types over six days. Each colour represents a different song type.

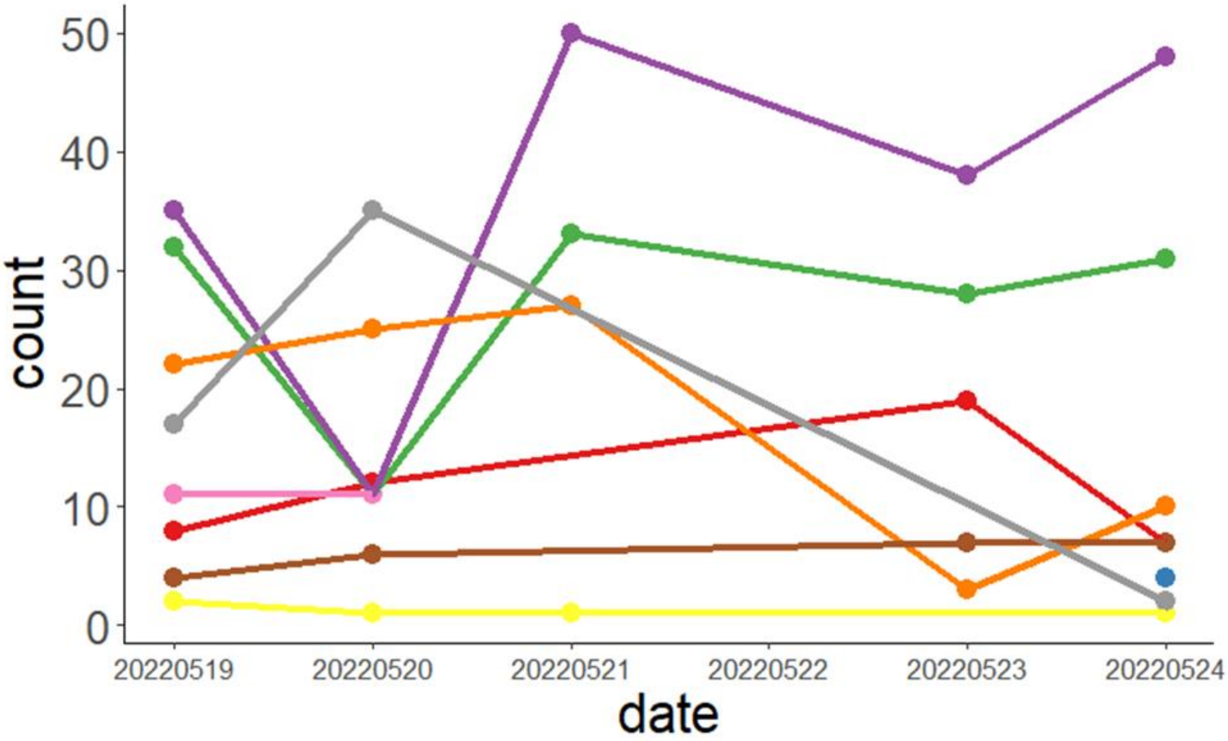

Figure 6: A line graph showing the count of nine of male OPR's song types over six days. Each colour represents a different song type.

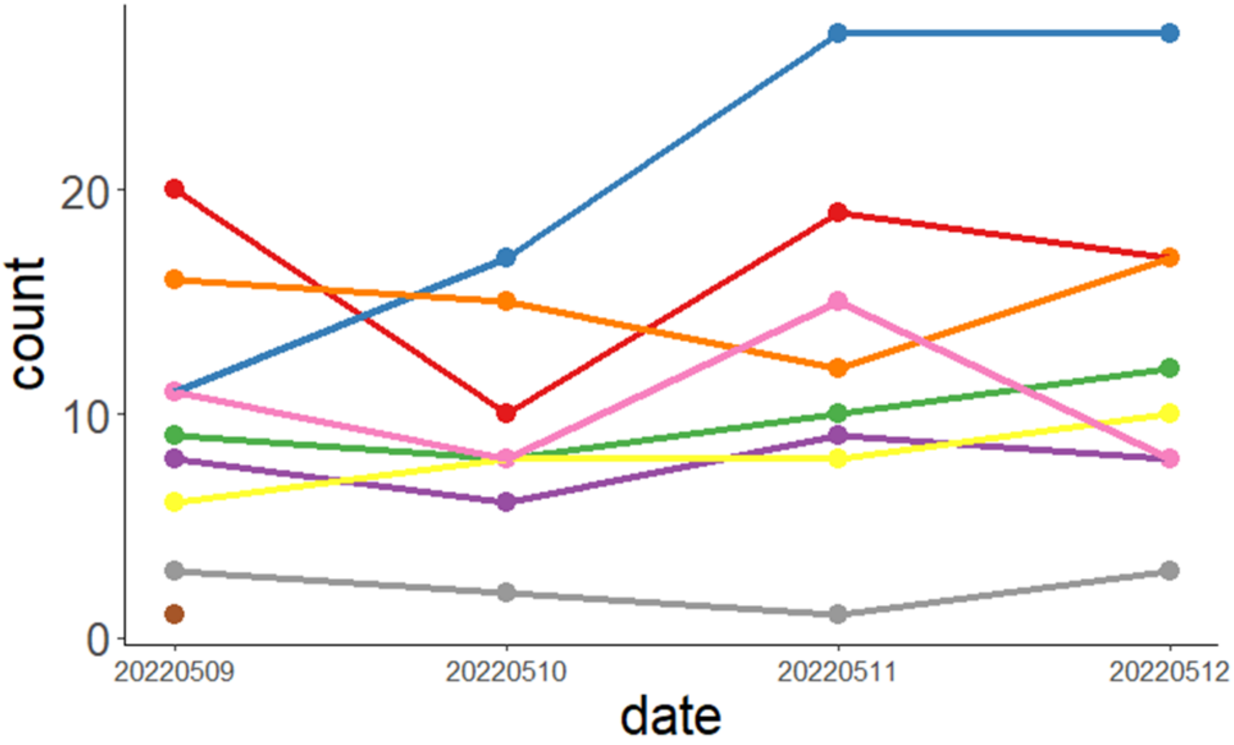

Figure 7: A line graph showing the count of nine of male LpRbTb's song types over six days. Each colour represents a different song type.

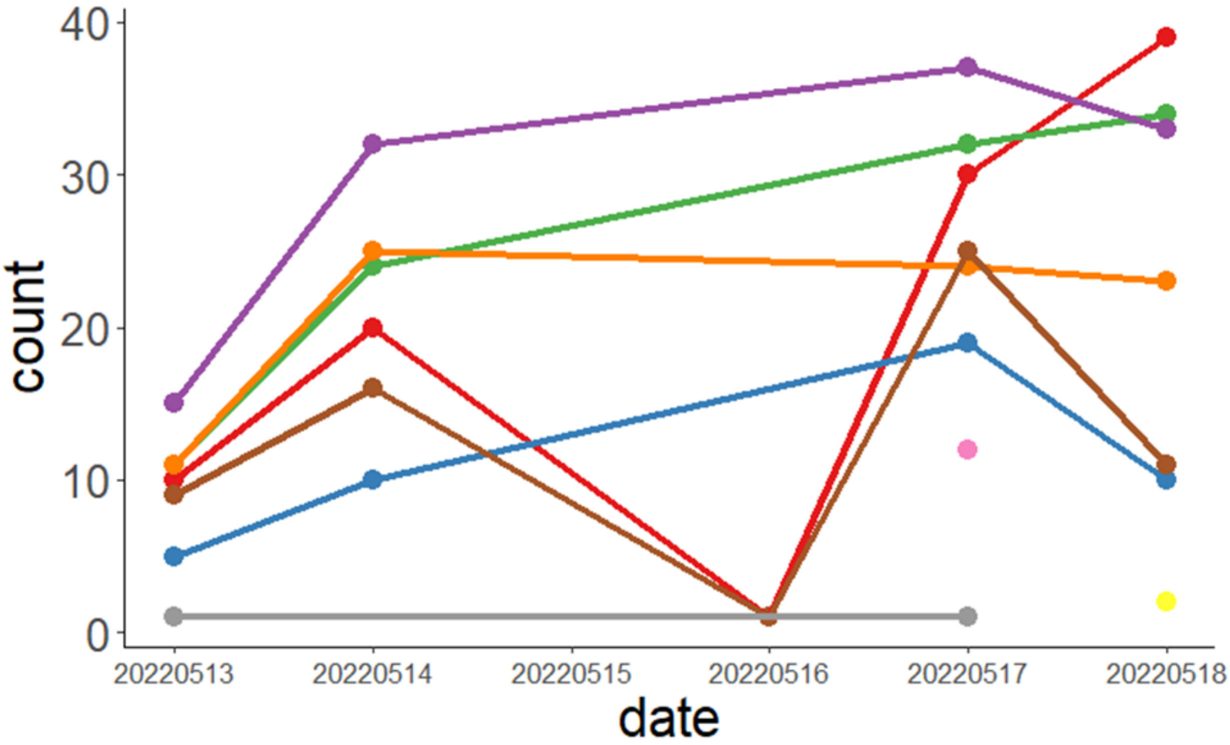

Figure 8: A line graph showing the count of nine of male LbOW's song types over six days. Each colour represents a different song type.

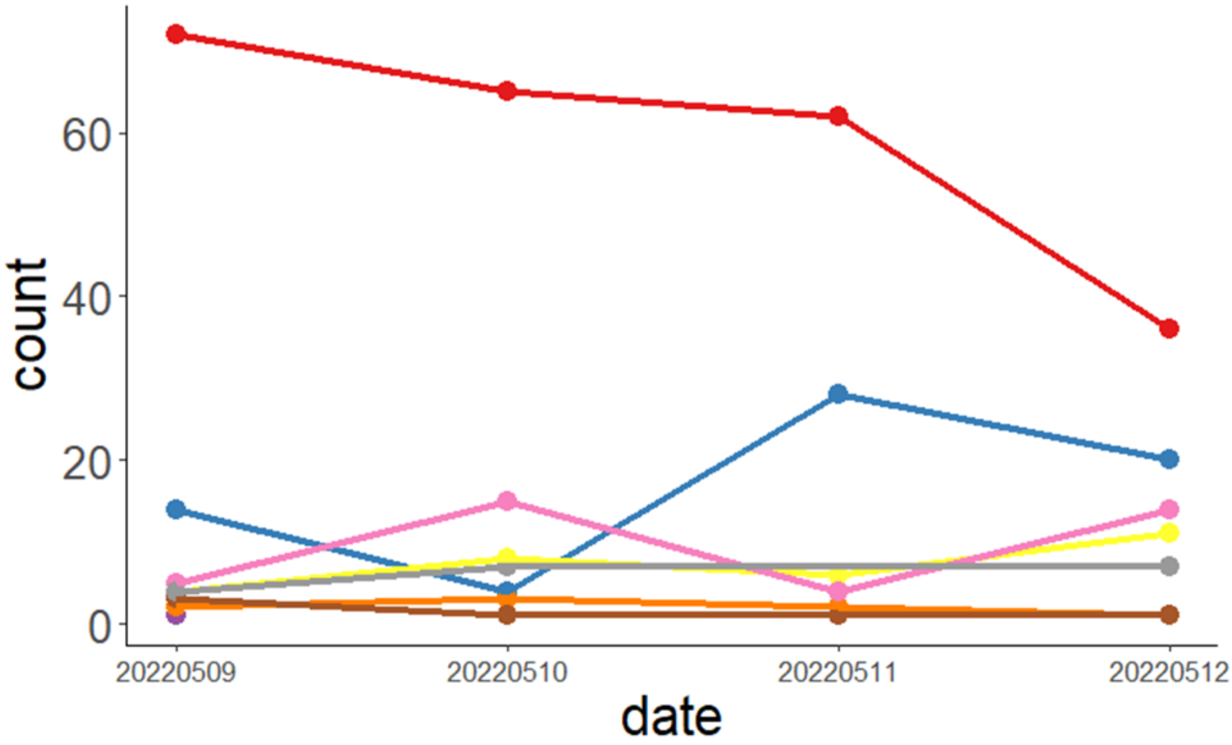

Figure 9: A line graph showing the count of nine of male LbLpY's song types over six days. Each colour represents a different song type.

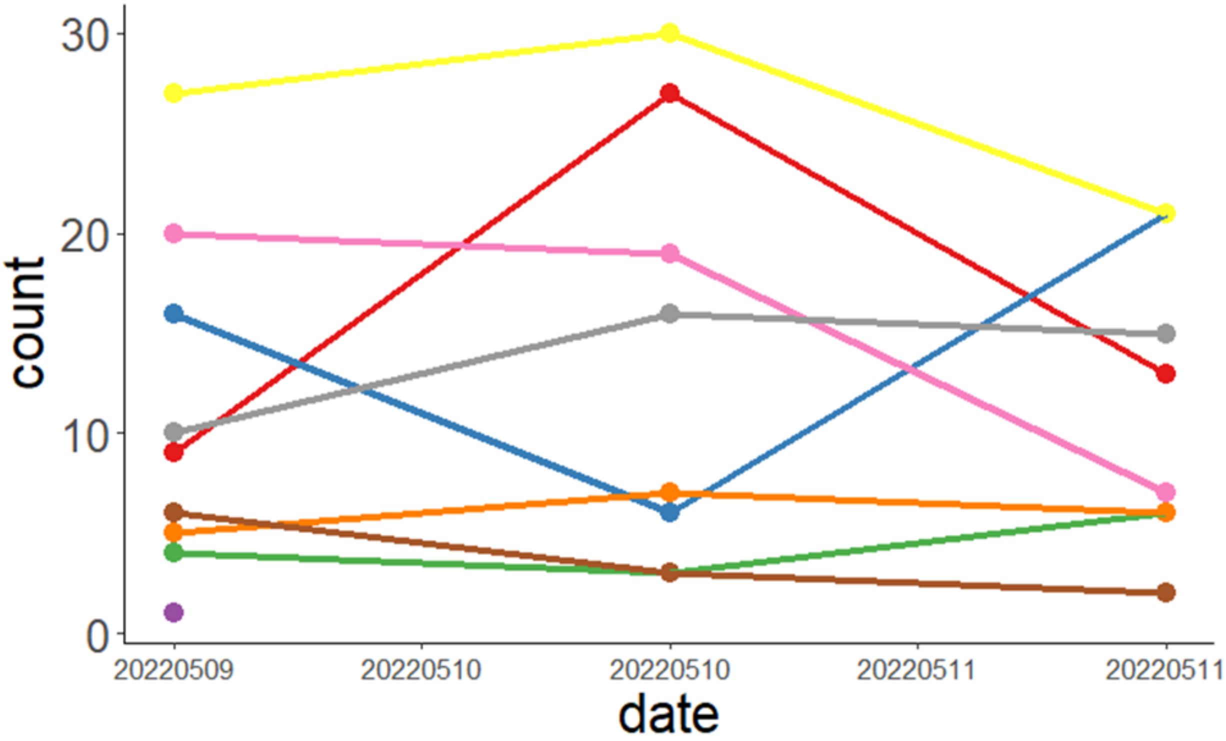

Figure 10: A line graph showing the count of nine of male KWY's song types over six days. Each colour represents a different song type.

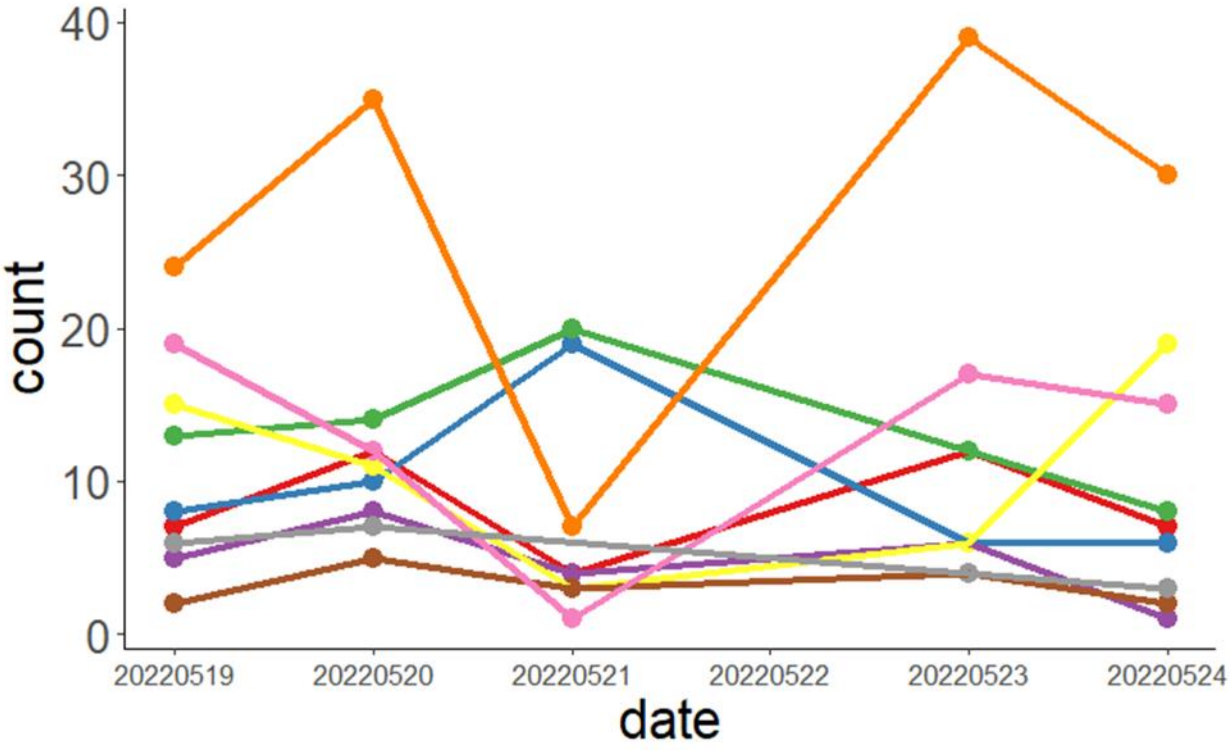

Figure 11: A line graph showing the count of nine of male KRDg's song types over six days. Each colour represents a different song type.

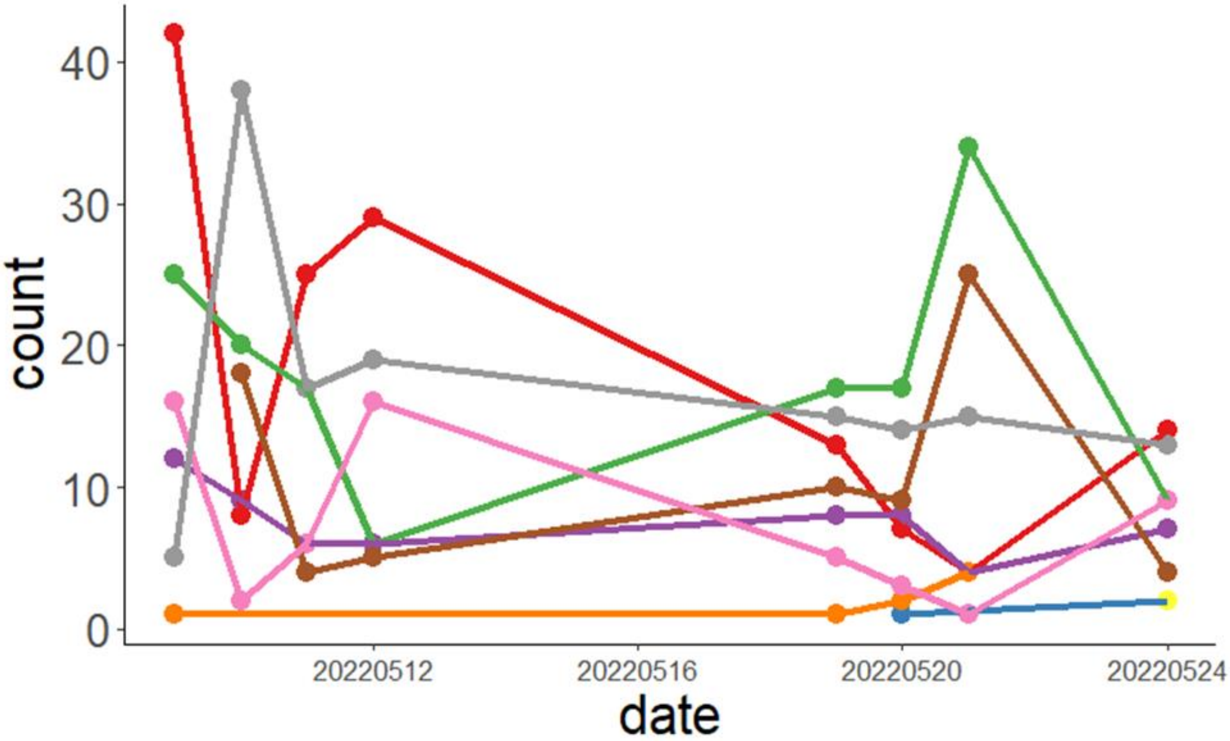

Figure 12: A line graph showing the count of nine of male KLgK's song types over six days. Each colour represents a different song type.

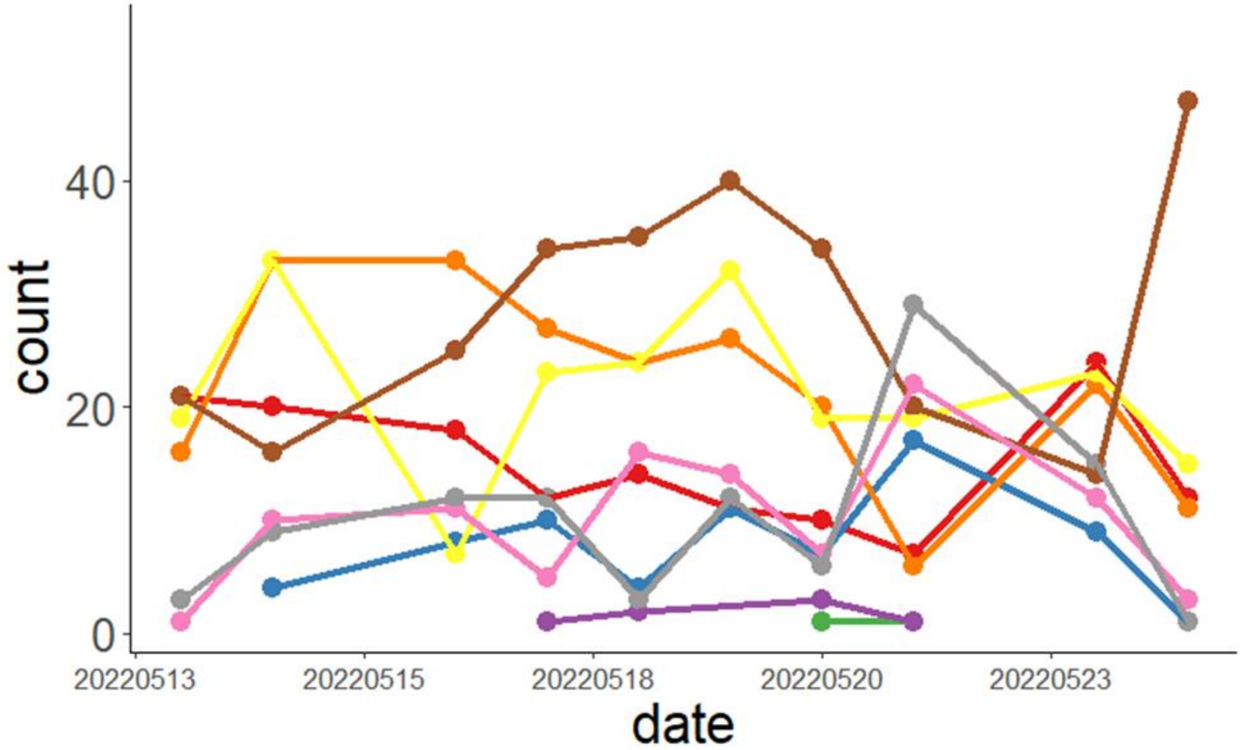

Figure 13: A line graph showing the count of nine of male DgTbO's song types over six days. Each colour represents a different song type.

APPENDIX 5: Posterior predictive check in the consistency of song type preference analysis

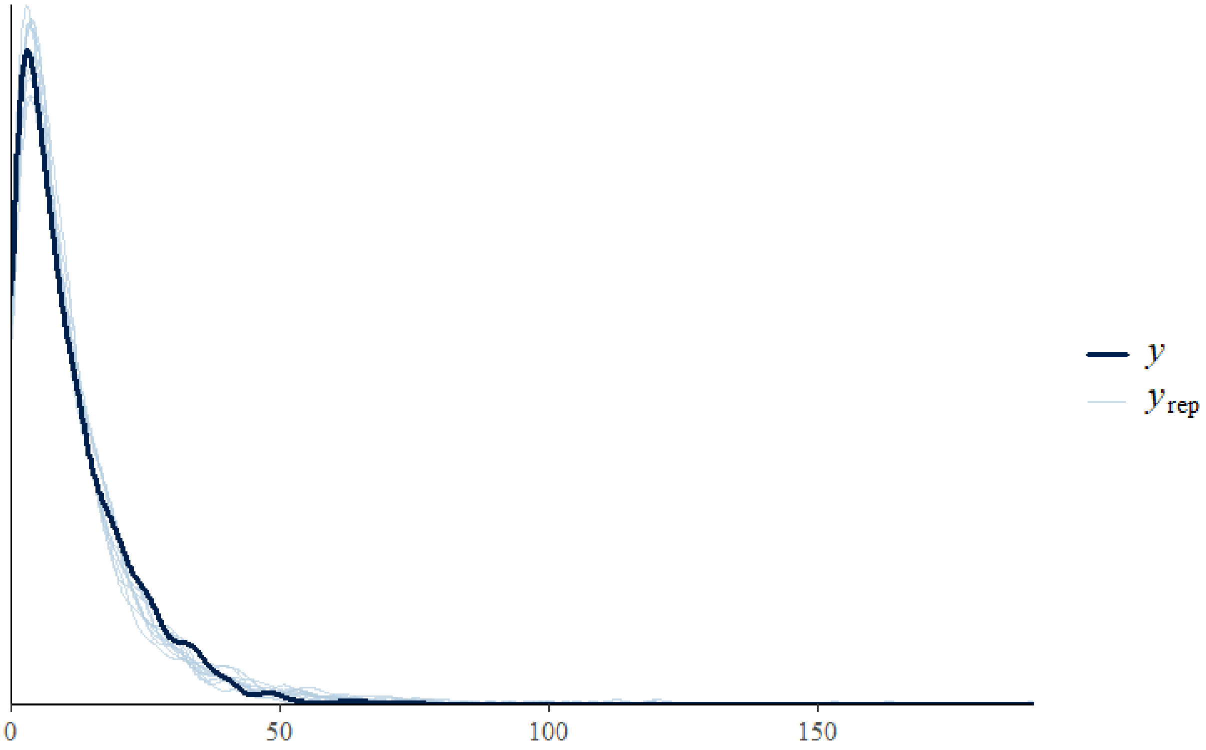

Figure 1: Example of a posterior predictive check. This is the output from the model of consistency of song type preference. The light blue lines (Yrep) represent generated samples of posterior predictive distribution, and the dark blue line represents the distribution of the observed data (Y).