



## **A Need for Individual Data Analyses for Assessments of Temporal Control: Invertebrate Fixed Interval Performance**

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We outline several experimental variables and address the inconsistencies of these variables within the invertebrate fixed interval literature. We posit some previous inconsistencies within the invertebrate fixed interval literature may be due to the utilization of aggregate versus individual analyses and contend the latter are critical in order for conclusions to be made about species' abilities to emit responses that can come under temporal control. To exemplify these statements, we exposed honey bees *Apis mellifera lingustica* ( $N = 13$ ) to either an FI 15 s or FI 30 s schedule of reinforcement and analyzed subjects' cumulative response records, response bin levels (i.e., the number of responses in each equal division of the fixed interval), quarter lives (i.e., when the first quarter of the trial's responses occurred in the fixed interval), inter-response time patterns, response duration patterns, and trial durations. No measures clearly indicated individual subjects' responding came under temporal control of the fixed interval schedules; however, pooled group analyses did produce seemingly clear evidence of temporal control.

Fixed interval schedules of reinforcement are one of the most basic assessments of temporal control and arbitrary timing. In the fixed interval protocol, responding is not reinforced until a prescribed interval of time has elapsed, and the first response after the interval elapses is reinforced (Ferster & Skinner, 1957; Skinner, 1938). From Skinner's perspective, responses occurring later in the fixed interval are more likely to be reinforced and thus occur in higher numbers whereas responses early in the fixed interval are less likely to be reinforced and thus occur in smaller numbers. Assuming fixed intervals that are longer than continuously reinforced (i.e., each response is reinforced) inter-response times are utilized, after extensive exposure to the fixed interval, vertebrate responding can traditionally be characterized by positively accelerating response levels (a *scallop* in the cumulative curve response record) or by a period of no responding followed by a period of steady responding (a *break-and-run* cumulative curve response record). Following Skinner's example, an assumption that all organisms produce similar response patterns became firmly rooted in early behavioral investigations even though fixed intervals had only been conducted with rats and pigeons. It was not until Myers and Mesker (1960) exposed a horse, Eskin, and Bitterman (1960) exposed African mouthbreeders, and Ginsburg (1960) exposed budgerigars to fixed interval schedules of reinforcement that comparative psychologists began assessing a wider range of species.

In the fixed interval literature, the vast majority of investigated species have been vertebrates; only three fixed interval assessments have been published using invertebrates, and these investigations have only been limited to bees. Grossmann (1973) investigated honey bees' responding and reported individual subject cumulative response records that did not contain scallops or break-and-runs. Boisvert and Sherry (2006) investigated bumble bees' responding and published post-reinforcement pause mean comparisons that supported the conclusion longer intervals produced longer post-

reinforcement pauses. Boisvert and Sherry (2006) also included a proportion of maximum response rate bin analysis as well as a *burst* assessment, and both measures were taken to indicate bumble bee responding was temporally controlled. Most recently, Craig, Varnon, Sokolowski, Wells, and Abramson (2014) investigated honey bee responding on fixed interval schedules by assessing both post-reinforcement pauses and response levels of the first half versus the second half of the fixed interval; Craig et al. (2014) did not observe response levels were higher later in the interval and did not observe individual cumulative curves contained scallop or break-and-run response records. Thus, at present, Boisvert and Sherry's (2006) bumble bees appear to have emitted responses that came under temporal control while the honey bees investigated by Grossmann (1973) and Craig et al. (2014) did not emit responses that demonstrated invertebrate timing.

Based on the invertebrate fixed interval literature, a potential species difference in temporally controlled responding may be present if species were to be indirectly compared across publications and research teams. However, while the fixed interval schedule is a basic protocol, at least eleven distinct environmental variables must be considered in comparative fixed interval analyses beyond the initial species difference that draws the majority of comparative psychologists' interest. Failure to properly control these variables renders direct species comparisons difficult at best, and impossible at worst. The comparative psychologists' core interest in species differences requires consideration of these eleven distinct variables.

In addition to facilitating species comparisons, understanding the effects and interactions of these instrumentation (viz., procedural) concerns is important from a traditional behaviorist paradigm. Inter-trial response variability when responding is reinforced on fixed interval schedules of reinforcement has been discussed in detail since the schedule's invention. While seemingly random or impossible to predict, Hoyert (1992) posits temporally controlled responding functions under a chaotic (i.e., deterministic) system. Thus, understanding the initial conditions and refining an instrumental or procedural control must be a major focus for not only comparative temporal investigators, but also for temporal control researchers investigating traditional animal models. Without having a complete understanding of the initial conditions and utilized instrumentation for each subject, temporal control researchers will be unable to account for the response variability within and between trials of fixed interval schedules of reinforcement.

Richelle and Lejeune (1980, 1984) recommend three strategies to assess temporal control. First, comparative psychologists must investigate a greater number of species. Prior to 1960, only rat and pigeon responding was investigated on fixed interval schedules. During the 1960s, a series of comparative fixed interval investigations were conducted in a variety of animals; during the 1970s, interest in drug research motivated primate research; however, by the mid-1980s, comparative fixed interval investigations were neglected. The following investigators were the first to contribute to the comparative temporal control literature for each species; Table 1 summarizes these comparative findings: Eskin, and Bitterman (1960) investigated African mouthbreeders; Waller (1961) investigated beagle dogs; Ferster and Zimmerman (1963) investigated rhesus monkeys; Rozin (1965) investigated goldfish; Cloar and Melvin (1968) investigated quail; Rubin and Brown (1969) investigated rabbits; Haney, Bedford, and Berryman (1971) investigated ravens; Lejeune (1971) investigated cats; Powell (1972) investigated crows; Vander Weele and Abelson (1973)

investigated Mongolian gerbils; Grossmann (1973) investigated honey bees; Byrd (1973; 1975) investigated chimpanzees and baboons, Barrett (1976) investigated squirrel monkeys; Wenger and Dews (1976) investigated mice; Anderson and Shettleworth (1977) investigated golden hamsters; Todd and Cogan (1978) investigated black-tailed prairie dogs; Kleinginna and Currie (1979) investigated kingsnakes; Lejeune and Richelle (1982) investigated turtle doves; Laurent and Lejeune (1985) investigated freshwater turtles; Lejeune and Wearden (1991) investigated woodmice and African cichlids; Brunner, Kacelnik, and Gibbon (1992) investigated starlings; Brodbeck, Hampton, and Cheng (1998) investigated black-capped chickadees; Taylor, Haskell, Appleby, and Waran (2002) investigated domestic hens; Higa and Simm (2004) investigated beta Siamese fighting fish; Bosivert and Sherry (2006) investigated bumble bees; and Toelch and Winter (2013) investigated long-tongued bats. Of these investigated species, only turtles, turtle doves, kingsnakes, honey bees, and Eskin and Bitterman's (1960) and Gonzalez, Eskin, and Bitterman's (1962) African mouthbreeders have not provided response records that were used to support temporal control. Lejeune and Wearden's (1991) African cichlids produced inconsistent evidence of responding coming under temporal control.

**Table 1.**  
*Comparative fixed interval investigations*

Author	Species	Schedules	Measures/Findings
Myers & Mesker (1960)	Horse ( <i>Equus ferus caballus</i> )	FI 60 s => FI 90 s => FI 180 s	Scalloped cumulative response records
Ginsburg (1960)	Budgerigars ( <i>Melopsittacus undulatus</i> )	FI 30 s => FI 60 s => FI 120 s	Scalloped cumulative response records
Eskin & Bitterman (1960)	African mouthbreeder ( <i>Tilapia marcocephala</i> )	FI 60 s, FI 120 s, FI 240 s	Non scalloped cumulative response records
Waller (1961)	Beagles ( <i>Canis lupus familiaris</i> )	FI 180 s	Scalloped cumulative response records
Ferster & Zimmerman (1963)	Rhesus monkeys ( <i>Macaca mulatta</i> )	FI 240 s	Scalloped cumulative response records; long PRPs and low response rates
Rozin (1965)	Goldfish ( <i>Carassius auratus</i> )	FI 60 s	Increasing response levels across six bins
Cloar & Melvin (1968)	Japanese quail ( <i>Coturnix coturnix Japonica</i> )	FI 30 s, FI 60 s, FI 120 s	Scalloped cumulative response records
Cloar & Melvin (1968)	Bobwhite quail ( <i>Colinus virginianus</i> )	FI 30 s, FI 60 s, FI 120 s	Scalloped cumulative response records
Rubin & Brown (1969)	American Dutch Rabbits	FI 30 s, FI 180 s	Break-and-run cumulative response records; PRP

	<i>(Oryctolagus cuniculus)</i>		dependent on schedule length; response rate not dependent on schedule length
Haney, Bedford, & Berryman (1971)	White-Necked Raven ( <i>Corvus cryptoleucus</i> )	FI 240 s	Scalloped cumulative response records; low response rates
Lejeune (1971)	Cats ( <i>Felis catus</i> )	FI 120 s => FI 300 s => FI 600 s => FI 900 s	Increasing response levels across FI; long PRPs
Powell (1972)	Crow ( <i>Corvus brachyrhynchos</i> )	FI 60 s, FI 120 s, FI 240 s	Scalloped and break-and-run cumulative response records; low response rates; quarter life at 70% of FI; long PRPs
Vander Weele & Abelson (1973)	Mongolian gerbils ( <i>Meriones unguiculatus</i> )	FI 60 s => FI 240 s, FI 120 s => FI 360 s	Scalloped cumulative response records only on FI 240 s
Grossmann (1973)	Honey bees ( <i>Apis Mellifera</i> )	FI 6 s => FI 9 s => FI 12 s => FI 15 s => FI 20 s : FI 90 s	Non scalloped cumulative response records
Byrd (1973, 1975)	Chimpanzees ( <i>Pan troglodytes</i> )	FI 600 s	Scalloped and possible break-and-run cumulative response records; low response rates; quarter life at ~70% of FI
Byrd (1975)	Olive baboons ( <i>Papio anubis</i> )	Multiple FI 30 FI 600 s	Scalloped cumulative response records; low response rates; quarter life at ~70% of FI
Barrett (1976)	Squirrel monkeys ( <i>Saimiri sciureus</i> )	FI 300 s	Scalloped cumulative response records

**Table 1 (cont.)**

Comparative investigations

fixed interval

Wenger & Dews (1976)	Mice (C57BL/6J strain)	Multiple FR 30 FI 300 s	Scalloped cumulative response records
Anderson & Shettleworth (1977)	Golden hamsters ( <i>Mesocricetus auratus</i> )	FI 5 s => FI 10 s => FI 20 s => FI 30 s	Increasing response levels across 16 bins; long PRPs and temporally ordered adjunctive behaviors
Todd & Cogan (1978)	Prairie dogs ( <i>Cynomys ludovicianus</i> )	FI 30 s => FI 45 s => FI 60 s => FI 90 s => FI 120 s => FI 150 s	Scalloped and break-and-run cumulative response records; low response rates
Kleinginna & Currie (1979)	Florida kingsnakes ( <i>Lampropeltis getulus floridana</i> )	FI 30 s	High response rates; no clear difference in PRP compared to CRF performance
Lejeune & Richelle (1982)	Turtle doves ( <i>Streptopelia turtur</i> )	FI 120 s => FI 360 s => FI 480 s => FI 600 s	Uniform response levels across four bins; short PRPs; high coefficient of variation;

Laurent & Lejeune (1985)	Fresh water turtle ( <i>Pseudemys scripta elegans</i> )	FI 30 s => FI 60 s => FI 90 s	Uniform response levels across 2 and 10 bins
Lejeune & Wearden (1991)	Woodmice ( <i>Apodemus sylvaticus</i> )	FI 30 s => FR 45 s => FI 60 s => FI 120 s => FI 180 s => FI 240 s	Low coefficient of variation; coefficients of variation increase with longer schedules
Lejeune & Wearden (1991)	Tilapia African cichlid ( <i>Sarotherodon niloticus</i> )	FI 2 s : FI 20 s => VI 20 s : VI 60 s => FI 60 s => FI 90 s => FI 120 s	Increasing response levels across FI; high coefficients of variation
Brunner, Kacelnik, & Gibbon (1992)	Starling ( <i>Sturnus vulgaris</i> )	Modified Peak Procedure: FI 0.8 s, FI 1.6 s, FI 3.2 s, FI 6.4 s, FI 12.8 s, FI 25.6 s	Increasing response levels across FI; response levels peak approximately at FI schedule values
Brodbeck, Hampton, & Cheng (1998)	Black-capped chickadees ( <i>Parus atricapillus</i> )	Peak Procedure: FI 12.5 s, FI 37.5 s	Break-and-run cumulative response records for individual subjects (scallop for summed response records); response levels peak approximately at FI schedule values
Taylor, Haskell, Appleby, & Waran (2002)	Brown Leghorn Hens ( <i>Gallus gallus domesticus</i> )	Peak Procedure: FI 2 s => FI 5 s => FI 8 s => FI 15 s => FI 30 s => FI 60 s => FI 120 s => FI 240 s => FI 360 s	Low response rates; quarter life at 40% of FI; response levels peak approximately at FI schedule values
Higa & Simm (2004)	Siamese fighting fish ( <i>Betta splendens</i> )	FI 30 s => FI 120 s => FI 60 s => FI 240 s	Scalloped cumulative response records; break points increase with longer schedules; PRPs increase with longer schedules
Boisvert & Sherry (2006)	Bumble Bees ( <i>Bombus impatiens</i> )	FI 12 s, FI 24 s; mixed FI 6 s FI 36 s, mixed FI 12 s FI 36 s, FI 6 s => FI 36 s, FI 12 s => FI 36 s	Maximum response levels towards end of FI; longer PRPs during longer schedules; response bursts approximate FI schedules
Toelch & Winter (2013)	Long-tongued bat ( <i>Glossophaga soricina</i> )	Modified Peak Procedure: FI 5 s, FI 11 s, FI 20 s	Response levels peak approximately at FI schedule values

Second, Richelle and Lejeune (1980, 1984) recommend comparing closely related species rather than a wide variety of unrelated species. With this strategy, instrumentation concerns are reduced as similar procedures and automated apparatus can be utilized. For example, Cloar and Melvin (1968) compared two species of quail (Bobwhite quail and Japanese quail) and observed similar performances between species using the same apparatus. Moreover, Lejeune and Wearden (1991) report comparisons between pigeons and turtledoves as well as comparisons between woodmice and rats. Lejeune and Wearden's (1991) coefficient of variation measure indicated pigeon responding came under greater temporal control of the fixed interval schedules than turtle dove responding and revealed striking similarities between woodmice, rats, and cats. As analyzing similar species facilitates similar

instrumentation protocols, direct comparisons are easier to make compared to the first strategy of comparing multiple, unrelated species. Evidence to support an additional distinction between the training of radical behaviorists and true comparative psychologists is that, of the wide range of pigeon and rat breeds that have been investigated, no direct comparisons between breeds have been made in either species. Often, fixed interval researchers will simply identify that *rats* or *pigeons* were the models of the investigation and not identify which breed of rat or pigeon was used. If breed differences are observed via Richelle and Lejeune's (1980, 1984) second strategy, archival researchers will be unable to properly evaluate several notable fixed interval publications due to lax descriptions of the animal models.

Third, Richelle and Lejeune (1980, 1984) recommend refining instrumentation to make direct species comparisons more possible. Thus, attempting to equalize these different environmental variables is critical for comparative investigations. The refinement of instrumentation in the comparative fixed interval literature has been discussed by previous authors, but no publications discuss more than a few possible instrumentation concerns. Laurent and Lejeune (1985) and Higa and Simm (2004) identified five separate considerations comparative psychologists must address, and we offer six additional considerations that may complicate direct species comparisons.

## **Instrumentation Considerations**

First, the response under investigation must be considered; the assumption that operant responding is similar across responses is likely false and serves to undermine parsimony concerns. When considering the traditional vertebrate animal models, a key-press in a pigeon is a fundamentally different operant behavior than a lever-press in a rat, yet direct comparisons have been attempted despite the different topographies of these behaviors (e.g., Lowe & Harzem, 1977). Within the invertebrate fixed interval literature, three responses have been assessed in two species. In bumble bees (Boisvert & Sherry, 2006), a proboscis extension response was assessed whereas in honey bees (Craig et al., 2014; Grossmann, 1973), a head-entry response and a full-body-entry response were assessed, respectively. Immediately, even when considering the similarity of the investigated invertebrate species, a direct comparison of operant learning becomes difficult. However, compared to other typical responses (e.g., a lever-press), the invertebrate fixed interval literature is relatively consistent.

A second instrumentation concern identified by Laurent and Lejeune (1985) and Higa and Simm (2004) is the utilized reinforcer. All invertebrate fixed interval investigations have reinforced responding with a 50% sucrose solution, so within this subset of the temporal control literature, sufficient control has been established for this variable. In the vertebrate fixed interval literature, many reinforcers (and shock as a punisher) have been used, but the majority of reinforcers have been consummatory (e.g., grain, pellets, milk). Investigating other reinforcing stimuli will be a worthwhile endeavor for invertebrate fixed interval researchers that are interested in studying invertebrates that are not bees.

A third instrumentation concern is the number of trials, or reinforcers, per session and per individual. Even if all species may be able to emit temporally controlled responses, the speed of acquisition of temporal control may vary greatly between species; as such, selecting an appropriate number of trials and thus exposures to the

fixed interval schedules is paramount. Within the invertebrate fixed interval literature, Boisvert and Sherry (2006) controlled the number of trials per session while Grossmann (1973) and Craig et al. (2014) did not. Relatedly, the number of hours of exposure to the schedule (a combination of number of sessions and number of trials) is an important instrumentation concern. Unfortunately, substantial exposure to fixed interval may be difficult for some comparative investigations. For example, a subject's lifespan or sleep/wake cycle could limit extensive exposure to fixed interval schedules.

A fourth instrumentation concern is the number of investigated fixed intervals, and the schedule durations used by the researcher. Throughout the fixed interval literature, FI 30 s, FI 60 s, FI 120 s, and FI 180 s appear to be the most commonly investigated schedule durations; however, FI 300 s, FI 600 s schedules are also present. Schedules over 15 min are less common, but sparsely appear throughout the literature (e.g., Cumming & Schoenfeld, 1958). Clearly, direct comparisons wherein a species' response patterns are compared with a second species' response patterns are impossible at different schedule durations; directly comparing response patterns of a crab on an FI 30 s with those of a crab on an FI 60 s is inappropriate, let alone with an octopus on an FI 60 s. Within the invertebrate fixed interval literature, relatively short fixed interval durations have been utilized. Grossmann (1973) investigated FI 6 s, FI 9 s, FI 12 s, FI 15 s, FI 20 s, and FI 90 s schedules; Boisvert and Sherry (2006) investigated mixed schedules of FI 6 s, FI 12 s, or FI 36 s; Craig et al. (2014) investigated FI 15 s, FI 30 s, FI 60 s, and FI 120 s. Interestingly, Craig et al. (2014) could not maintain responding at the longer FI 60 s and FI 120 s sessions. It is important to note short schedules have only been able to support conclusions of temporal control in invertebrates; if long fixed intervals cannot bring responding under temporal control, this may be an indication of poor levels of temporal trainability in invertebrates. Thus, fixed interval researchers may consider investigating longer schedules in order to be able to compare the invertebrate literature with vertebrate performances.

The final instrumentation consideration identified by Laurent and Lejeune (1985) and Higa and Simm (2004) is the drive-level, or motivating operation of the procedure. This instrumentation consideration is obviously related to the utilized reinforcer. For vertebrates, the typical motivating operation is to deprive subjects of food to 80% of their free-feeding body weight. For invertebrates, only non-deprivation procedures have been employed, and as bees are the only invertebrates that have been investigated, the natural foraging patterns as the bees fill and unload their social crops have been used as the motivating and abolishing motivations. Thus, individual bees encounter varying motivating operations based on individual crop-size differences; the experimenter does not control the number of trials per session. This is an important distinction that may complicate comparing invertebrate species' performances with those of vertebrates.

While Laurent and Lejeune (1985) and Higa and Simm (2004) provide separate, but overlapping, lists of important instrumentation concerns for comparative psychologists, these lists are not exhaustive and many other instrumentation considerations must be made. As mentioned previously, the number of trials is an important consideration, but the number of sessions is also an important consideration for the same reasons as considering the number of trials (viz., total exposure to the schedule). The primary concern regarding the number of sessions involves data analyses; *warm up* effects are often disregarded in favor of analyses of stable-state responding. Hence, it is important to consider which sessions will make up the data

analyses and thus how many sessions are required to assess temporal control. For example, Boisvert and Sherry (2006) analyzed the final three sessions whereas Grossmann (1973) reported nine FI 20 s and FI 90 s sessions (with varying numbers of training trials) while Craig et al. (2014) analyzed all FI sessions and directly compared the first and last session performances.

Moreover, the inter-session interval must be addressed. While Neuringer and Schneider (1968) manipulated inter-trial intervals via blackouts (i.e., lights in the operant chamber were turned off), only one systematic manipulation of inter-session interval has been conducted; Gleitman and Bernheim (1963) manipulated a test inter-session interval to either 24 hours or 24 days in an attempt to assess retention and long term memory. Longer inter-session intervals resulted in more responding early in the interval thus suggesting reduced temporal control. For free-flying bees, inter-session interval is difficult to experimentally control and can only be measured. Bees return to the hive after filling their social crops at the operant chamber, and once inside the hive, the subjects unload their social crops, and may engage in a variety of additional social behaviors before leaving the hive and returning to the operant chamber. Controlling this inter-session interval is impossible using this protocol and is an inherent aspect of working with a wild and unconfined species; regardless, this variability may impact between-session comparisons. Future invertebrate investigations may greatly benefit from utilizing observational hives and recording inter-session behaviors while subjects are in the hive.

Laurent and Lejeune (1985) and Higa and Simm (2004) discuss the importance of considering the utilized reinforcer; additionally, the impact of the amount of each reinforcer may be helpful to consider. Unfortunately, the fixed interval literature is punctuated with investigations that do not precisely measure the amount of reinforcement; rather than defining their reinforcer as a weight, a time of exposure to reinforcement will be provided (this is an indirect measure of consumed reinforcement). However, assessing the effect of the amount of each reinforcer is difficult, for doubling the size of the reinforcer between conditions adds confounds related to increasing the size of a consumable (e.g., more time required to consume the reinforcement, different stimulus properties associated with size). For these reasons, Guttman (1953) recommended assessing the impact of the amount of each reinforcer via systematic manipulations of reinforcer concentration. Thus, the stimuli properties related to reinforcement size are not affected by the concentration manipulation, and the amount of time to consume the reinforcement is not impacted by the manipulation. Lowe, Davey, and Harzem (1974) also assessed reinforcement concentration and found higher concentrations increase post-reinforcement pause, but not average response rate; thus, higher concentrations improve temporal control, for longer post-reinforcement pauses and low average response rates have been taken to operationalize temporal control (e.g., Dukich & Lee, 1973; Ferster & Skinner, 1957; Hanson & Killeen, 1981; Todd & Cogan, 1978). Within the fixed interval invertebrate literature, a consistent concentration (50%) sucrose solution has been utilized; continuing this trend is advisable, and varying reinforcement concentration may help address concerns related to reinforcement property artifacts in a simple manner. Additionally, manipulating the subjective *value* of a foraging location may be interesting from a more ecological perspective.

An additional concern is that multiple protocols are inconsistently used within the fixed interval literature. The most basic protocol difference is the utilization of between-

subject or within-subject protocols and condition assessments. The within-subject protocol often incrementally increases the fixed interval schedule duration (e.g., condition 1 is an FI 0 s, condition 2 is an FI 3 s, condition 3 is an FI 30 s, condition 4 is an FI 90 s). The between-subject protocol tends to assess the immediate shift from a baseline performance to a specific fixed interval schedule (e.g., group 1 is tested on an FI 30 s and group 2 is tested on an FI 90 s). Within the invertebrate fixed interval literature, Grossmann (1973) utilized an incrementally increasing (within-subject) protocol while Boisvert and Sherry (2006) and Craig et al. (2014) have utilized an immediate shift (between-subject) design.

A second protocol difference is if simple or compound schedules are utilized. Grossmann (1973) and Craig et al. (2014) assessed simple FI schedules of reinforcement while Boisvert and Sherry (2006) assessed a compound (mixed) schedule. As invertebrates have not clearly demonstrated evidence that their responding can come under temporal control of fixed intervals, we believe that simple FI schedules may initially be more illuminating than when compound FI schedules are investigated, for more complex protocols implicitly assume temporally controlled responding on simpler protocols. This assumption has not been substantiated for invertebrates. Boisvert and Sherry (2006) briefly report a preliminary simple FI investigation, but only provide a *p*-value and thus we cannot be assured this assumption is safe to make (as the authors seem to imply). Compound schedules (i.e., combinations of simple fixed interval, variable interval, fixed ratio, or variable ratio schedules) with FI components rose in popularity during the 1970s when these types of schedules were utilized to assess the specific effects of various drugs on behavior. As the invertebrate fixed interval literature is still in its infancy, we recommend publishing clear indications of temporal control on simple schedules, for complex schedules are difficult to compare across publications and research teams.

A third protocol difference is the onset of the fixed interval schedule within a session. Traditionally (Ferster & Skinner, 1957), reinforcement delivery or a short blackout period restarted the fixed interval schedule. This provides a clear stimulus for the subject, for reinforcement delivery is marked/signaled via mechanical sounds as reinforcement is delivered. However, others (e.g., Brunner, Kacelnik, & Gibbon, 1992; Mechner, Guevrekian, & Mechner, 1963; Shull, 1970) have utilized a response-initiated protocol wherein subjects reentered a fixed interval schedule after consuming the reinforcement and making a response. This protocol essentially subtracts the amount of time required to consume reinforcement from a post-reinforcement pause measure (more appropriately labeled as *latency* in a response-initiated protocol). Surprisingly, relatively few subsequent investigations using a response-initiated protocol have been conducted. Additionally, initiating a session with a continuously reinforced trial in order to initiate the first analyzed fixed interval trial is a small procedural difference that helps ensure responding is maintained for opportunistic species like bees.

A fourth protocol difference is the departure from the fixed interval procedure in favor of protocols related to Scalar Expectancy Theory (Gibbon, 1977) that has largely dominated the temporal control literature since its development. Examples of procedures related to Scalar Expectancy include Church and Gibbon's (1982) temporal generalization protocol, Stubbs' (1976) temporal bisection task, and Catania's (1970) peak procedure. These protocols are extensions of the fixed interval, but a comprehensive comparison between methods has not been made. Comparative investigators face a major challenge when attempting to compare animal and human

timing performances, for most modern human investigations utilize temporal bisection or temporal generalization tasks while modern animal investigations utilize peak procedures (e.g., Brodbeck, Hampton, & Cheng, 1998; Cheng, Westwood, & Crystal, 1993; Taylor, Haskell, Appleby, & Waran, 2002; Toelch & Winter, 2013); however, peak procedures conducted with humans have revealed similarities between species (e.g., Rakitin et al., 1998). For invertebrate investigations, assessing higher levels of temporal control via procedures designed to assess Weber Law, or Scaling properties may not be fruitful if responding on simple FI schedules does not conform to vertebrate response records. Until clear evidence has been generated to support a conclusion that invertebrate responding can come under temporal control, simple procedural designs may be most beneficial for timing researchers.

An additional instrumentation concern is the marking stimuli used in the protocol. Multiple types of signals, or secondary reinforcers, have been used in fixed interval investigations to indicate a variety of procedural events. Reinforcement signaling is fairly common; when reinforcement becomes available, a light or sound will signal reinforcement delivery. This type of signal reduces reinforcement delays and should improve temporal control without impacting the fixed interval schedule with stimuli confounds. Ferster and Zimmerman (1963) extended Ferster and Skinner's (1957) investigations with signals for the remainder of the fixed interval (using what were essentially physical clocks); both investigations found signals improved temporal control, but teasing apart the effect of physical discrimination with temporal discrimination is not possible with a marking procedure. Clearly, carefully selecting marking stimuli is an important task for comparative researchers. Within the invertebrate fixed interval literature, Grossmann (1973) does not report marking stimuli; Boisvert and Sherry (2006) marked the initiation of the fixed interval and contingent response via lights; and Craig et al. (2014) marked non-contingent and contingent responses via apparatus vibrations. Thus, the invertebrate fixed interval literature does not use similar marking stimuli and may benefit from using consistent marking stimuli.

The final instrumentation consideration concerns dependent variables and their analyses. In order to make claims about species' differences, standardizing the operationalization of *temporal control* is paramount. Zeiler and Powell (1994) attempted, as have others, to establish an operational definition of temporal control, but these attempts at standardization have largely been ignored in favor of an unsystematic assessment of a variety of dependent variables across research teams. The fact remains that many different dependent variables and data analyses have inconsistently been used to infer, or reject, temporal control. Rather than limit which dependent variables should be used to infer temporal control, we recommend comparative investigators conduct multiple assessments of each of the common operationalizations of temporal control. Within the invertebrate fixed interval literature, Grossmann (1973) reported individual cumulative response curves, Boisvert and Sherry (2006) analyzed post-reinforcement pauses, response rates, and *response bursts*, and Craig et al. (2014) reported a response level bin analysis and a post-reinforcement pause analysis.

## **Individual versus Aggregate Analyses**

Relatedly, the method of analysis of these dependent variables is an important consideration, and a central issue is if aggregate or individual analyses are employed.

Branch and Gollub (1974) famously cautioned against the use of aggregates for response rate analyses, for individuals exposed to extensive numbers of fixed interval trials tend to exhibit break-and-run patterns of responding (Cumming & Schoenfeld, 1958; Schneider, 1969) whereas aggregating response rate distributions produced artifact scalloped cumulative curves. However, given the scallop has been observed in individual subject trials (e.g., Ferster & Skinner, 1957), it is possible that averaged scallops are not always artifacts and may truly represent individual performances. Surprisingly, after Branch and Gollub (1964), relatively few temporal control publications have performed individual trial or subject analyses, though notable exceptions exist (e.g., Balci et al., 2008; Balci, Ludwig, & Brunner, 2010; Cheng & Westwood, 1993; Church, Mack, & Gibbon, 1994).

The focus of science on particulars (i.e., individuals) versus universals (e.g., aggregates) is a long-standing philosophical discussion (Franck, 1986). Radical behaviorists initially seemed to value focusing on individuals; indeed Mace and Kratochwill (1986) single out behaviorists as the only psychology researchers with a rich history in individual subject analyses. However, this individual focus may have been a result of practical instrumentation limitations due to qualitative analyses surrounding response cumulative curves rather than theoretical reasons; following Schneider's (1969) quantitative measurement of inter-response times, aggregating individual subject's data and focusing on group aggregates became common for behaviorists. While focusing on aggregates may be an important scientific endeavor for temporal control researchers, small subject sizes and few replications in most investigated species render focusing on individuals and particulars to be preferable as current practices severely limit generalizing to universals. The current temporal control literature uses inter-individual methods to describe learning and temporal control even though these attributes can only occur within individuals as aggregates do not exist in reality; aggregates cannot emit behaviors or learn, let alone emit behaviors that come under temporal control. This disconnect between behavior methods and theory is important to address.

We contend that focusing on individual observations is important for several reasons from an Aristotelian philosophical realist framework; this perspective counters the positivism that has historically dominated the majority of behavioral research. Aristotelian metaphysics and realism focuses on observations that occur in reality without an observer; individuals can occur in reality, but aggregation requires an observer to perform the abstraction. First, learning (and temporal control) occurs in an individual organism, not in an aggregate, or in a population parameter. Focusing an analysis on observations (i.e., the organism) is more realistic than focusing an analysis on an abstraction (e.g., an aggregate). Individual subjects actually exist whereas aggregate abstractions do not exist outside of an observer's perception. Second, group aggregates can misrepresent individuals; this is the main concern voiced by Branch and Gollub (1974) regarding individual break-and-run response records being averaged into scalloped response records. Aggregate analyses suffer from concerns regarding outlier effects, or artifact trends that do not represent individuals in a group. Third, aggregates are often taken of discrete measures even when doing so violates the permissibility of Stevens' (1946) outlined scales of *measurement*. Indeed, responses are a discrete quantitative process and occur on an ordinal scale (at best). In order to be considered continuous, properties must satisfy a density (i.e., resolution) requirement such that an infinite number of divisions of a measure can be made; for example, meters are continuous, but responses are not (Michell, 1994, 1997). In order for multiplicative

properties to be appropriate, scales of measurement must be continuous (e.g., Stevens' (1946) interval and ratio scales). The concept of a half a response is nonsensical and is not based in realism; thus, the idea of an average 1.5 responses being emitted per time interval (i.e., a 1.5 response rate) is also not realistic. However, the behaviorist literature is dominated by aggregate response rate analyses despite these methods not being based in realism. Fourth, a divergence exists within psychology as aggregate methods are utilized to infer individual theoretical conclusions. Realistic and individual observations are often taken to an abstract aggregate level. However, if only these aggregates are analyzed, the researcher cannot make claims about individual subjects and can only comment on the analyzed abstractions, and the population parameters that have been estimated from these abstractions; models using aggregation to make inferences about individual subjects rather than a population parameter are not realistic. For these reasons, we recommend assessing and reporting individuals' response patterns as an indicator of temporal control.

Fixed interval schedules are infamous for their highly variable effects on behavior; coupling this variability with the inconsistencies observed in invertebrate species' behaviors (e.g., Dinges et al., 2013) especially adds to concerns related to the possibility of unrepresentative aggregates. Clearly, assessing learning in individuals is paramount, so we recommend using data analyses methods that remain grounded in observed individual data and do not rely on aggregate analyses. Indeed, many of the assumptions (e.g., normality, homogeneity, independence, continuity) required to perform traditional null hypothesis significance testing are not met by behavioral data (Craig et al., 2012; Laurent & Lejeune, 1985); individual analyses may be required.

Clearly, the invertebrate fixed interval literature can benefit from a series of instrumentation considerations. In the present manuscript, we performed a realistic, individual analysis of several measures of temporal control for honey bee responding. To eschew the methodological difficulties associated with relying on aggregate analyses, the collected data were assessed by using a series of ordinal analyses from an Observation Oriented Modeling paradigm (Abramson, Craig, Varnon, & Wells, 2015; Craig et al., 2012, 2014; Dinges et al., 2013; Grice, 2011, 2014). For a comparison of traditional statistics compared to Observation Oriented Modeling, see Dinges et al. (2013). Using Observation Oriented Modeling, the individual's observed data can be compared to an ordinal prediction (i.e., an ordered a priori hypothesis), and a series of randomizations of the observed data can be compared to the ordinal prediction to determine if the observed data differ from the randomized data sets.

## **Method**

### **Subjects**

Subjects were wild free-flying *Apis mellifera* L. (N = 13) from the Oklahoma State University Comparative Psychology and Behavioral Biology Laboratory apiary; Oklahoma State University does not require ethics board approval for invertebrate investigations, so the reported procedures are in accordance with institutional ethical standards. During the experiment, subjects flew from their hive to forage in an operant chamber (Sokolowski & Abramson, 2010). All subjects were experimentally naïve prior to the experiment.

### **Apparatus**

We utilized two adjoined computer-controlled clear acrylic operant chambers (24 cm × 26 cm × 38 cm) that provided 50% sucrose solution. The operant chambers were located approximately 3 m from a 10% sucrose solution feeding station. The top of an operant chamber served as a door the experimenter opened and closed once the subject attempted to enter or leave the apparatus. Once inside the operant chamber, subjects entered a response hole (diameter: 5 mm) located in the center of the side of the apparatus opposite of the adjoining wall separating each operant chamber. A response was recorded when the subject entered the response hole in the operant chamber and broke an infrared beam located 1 cm within the response hole. The response was considered complete when the subject exited the response hole. To make multiple responses, the subject was required to repeatedly enter and exit the response hole. When reinforcement contingencies were met, 5 $\mu$ l of 50% sucrose solution was released via a computer-controlled stepper motor into a cup attached to the end of the response hole located in front of the subject's head while she was still inside the response hole. The stepper motor served as a consistent marking stimulus, for the motor lightly sounded and vibrated the apparatus upon reinforcement delivery. A visualization of the apparatus is displayed in Figure 1.

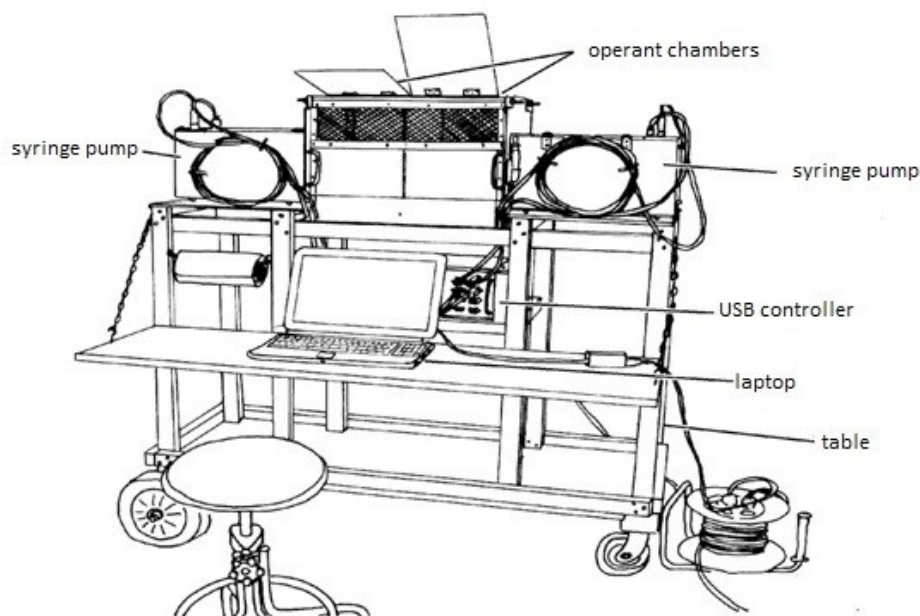


Figure 1. Honey bee apparatus.

## Shaping

Subjects were randomly collected from the 10% sucrose solution feeding station and were brought to the operant chamber where hole-entering responses were shaped. During shaping, drops of sucrose solution were placed near the response hole, and then inside the response hole. Shaping was considered complete once the subject freely responded by entering the response hole and consistently returned to the operant chamber directly from the hive. After shaping, each subject was tagged so the subjects could be distinguished. We used a Queen Marking Tube (a small Plexiglas cylindrical tube with an open end opposite a plastic grate), and a foam plunger to trap and immobilize the subject against the plastic grate while a colored, numbered tag was attached with a non-toxic adhesive; these materials were purchased from Betterbee (Greenwich, NY).

## Sessions

We utilized the foraging patterns of our free-flying honey bees to separate sessions; we collected all session data for each subject in a single day. Each visit to the apparatus after returning from the hive was considered a separate session. Throughout the experiment, a session was initiated by a subject's first response in the operant chamber after returning from the hive. Each session ended as the subject completed its final response prior to returning to the hive; we waited until the subject returned to the hive

before considering a session complete. As each session's duration was determined by the subject's behavior, session durations were not identical. In addition to variable session durations, we did not control the number of trials per session. Honey bees can hold between 50  $\mu$ l to 80 $\mu$ l of solution and return to the hive to unload after filling their social crop; hence, each session could offer anywhere between 10 to 16 reinforcers, though many sessions contained fewer than 10 trials. This variability in the number of reinforcers per session is an inherent aspect of working with unconfined and wild subjects in a naturalistic setting.

If a subject left the operant chamber during a session, we visually followed the subject to determine if she returned to the hive or the nearby 10% sucrose solution feeding station. If the subject returned to the hive, the session was considered complete, and another session began when the subject returned to the operant chamber. However, if the subject returned to the 10% sucrose solution feeding station and extended its proboscis or did not return to the operant chamber after 30 min, data collection was terminated for that subject to prevent schedule contamination and control the upper limits of the inter-session interval.

Sessions began after hole-entering responding was shaped and subjects directly returned to the operant chamber after leaving the hive. All subjects completed the 27 sessions in one day. We did not collect data over multiple days because we were unable to confine our subjects to assure subjects were not foraging at different locations and thus experiencing different reinforcement contingencies between days. However, we were able to ensure subjects were only foraging at the operant chamber throughout the experiment, for we visually followed subjects to be sure they returned to the operant chamber immediately after leaving the hive. We recorded response duration and inter-response time (IRT).

## **Baseline**

Six baseline sessions of continuous reinforcement (CRF) were administered so that each bee could serve as her own control. During baseline sessions, subjects were allowed to freely enter the operant chamber, respond, and exit the operant chamber to avoid potential post-reinforcement delay effects (Craig et al., 2012).

## **Fixed Interval Schedules**

After six sessions of baseline CRF were completed, subjects entered the experimental condition for 20 sessions wherein responding was reinforced on either an FI 15 s ( $n = 8$ ) or FI 30 s ( $n = 5$ ) schedule of reinforcement.

## **Groups**

Subjects were randomly assigned to two groups of differing FI schedules with 10 subjects in each group; only 13 subjects finished the experiment. The first six sessions were baseline continuous reinforcement sessions. Following the six baseline sessions, 20 FI sessions were administered; FI schedule duration served as the only manipulated difference between groups. The groups were named according to the conditions and FI schedule to which subjects were assigned and serve to indicate the utilized AB repeated measures design: 0-15, 0-30. The first number represents the CRF baseline (an FI 0 s schedule) and the second number represents the FI schedule of the experimental condition (i.e., the group assignment).

We only assessed subject responding if the subject initiated the final fixed interval session. Only eight subjects in the 0-15 group initiated the final fixed interval session while only five subjects in the 0-30 group initiated the final fixed interval session.

## **Data Analysis**

In an attempt to return temporal control investigations to concerns of particulars (e.g., individual subjects) rather than universals (e.g., population parameters), we used Observation Oriented Modeling (Grice, 2011, 2014) which is a data analysis technique that permitted us to compare our observed results to expected patterns of outcomes for each subject and then to evaluate the differences with an accuracy index and a randomization test. Observation Oriented Modeling (OOM) assesses individual observations and does not rely on traditional summaries of data such as measures of central tendency or variability. By using these methods, we were able to eschew the assumptions of null hypothesis significance testing (e.g.,

homogeneity, normality) as well as avoid construing temporal control as an abstract population parameter such as a mean or variance to be estimated from our data.

Within OOM, we performed a series of ordinal analyses that produce a percent correct classification (PCC) value and a chance-value (a probability statistic). For each analysis, an observed PCC value was computed by comparing an a priori ordinal prediction with the observed data. The resulting PCC value ranges from 0 to 100 and is the percent of the observed data that matches the expected ordinal pattern. Higher PCC values indicate more observations were correctly classified by the prediction. The PCC value is a 2-order assessment; when more than two orders are assessed, OOM also provides a complete percent correct classification (CPCC) value which indicates the extent the full prediction is met. The CPCC value becomes an increasingly conservative assessment as more orders are used for an analysis. We did not utilize imprecision values for any of the conducted OOM analyses.

Next, a randomization process wherein the observed data were randomly shuffled between groups/conditions was repeated 100 times for each ordinal analysis; these randomized datasets were each compared to the original ordinal prediction to create a range of randomized PCC values. To facilitate interpretation of the PCC value, the minimum and maximum randomization PCC values are reported. The randomization ranges are especially helpful when considering assessments of three or more orders; increasing the number of orders produces smaller randomization ranges with maximum randomization PCC values that are rarely larger than zero for more than 5-order ordinal assessments.

The observed PCC values were then compared to the randomized range of PCC values to compute a chance value (*c*-value). The *c*-value ranges from 0 to 1 and displays the proportion of randomized versions of the observed data that yielded PCC values greater than or equal to the observed data's PCC value. For example, a *c*-value of .01 indicates the observed PCC value was larger than 99 of the PCC values obtained from 100 randomized versions of the data. As *c*-values are calculated from randomizations of the observed data points, each PCC value is assessed on an adaptable distribution that is based on observed data rather than a hypothetical distribution (e.g., the standard normal curve).

## Results

Previously, others and we (Dukich & Lee, 1973) have recommended that researchers assess multiple measures of temporal control. In the following sections, we report honey bees' performance on six measures of temporal control. The full results of all of the performed assessments are contained in a series of supplemental tables and figures; throughout the following sections, we will highlight the general trends for individuals and groups, and we discuss exceptions to these trends.

### Cumulative Response Curve Analysis

Figure S1 through Figure S13 in the supplementary figures display individual subject cumulative curves for the final FI trial for all subjects. Most honey bees that initiated the final fixed interval session (i.e., session 26) displayed cumulative response records that indicated responding did not come under temporal control. Instead, responding was better characterized as either a *consistent* or *break-through* response pattern; neither pattern is indicative of temporally controlled responding. Only B3 and B10 in the 0-15 group and B7 and B9 in the 0-30 group emitted trials that resemble a scalloped or break-and-run response pattern.

### Response Bin Analysis

An increase in response levels as reinforcement availability approaches has been suggested to indicate temporal control (Weiss & Moore, 1956). To perform our response bin analysis, we divided each fixed interval into bins for each trial for subjects that completed their final fixed interval condition. We divided each trial's fixed interval into two bins, four bins, 10 bins, and 20 bins under the a priori prediction that response tallies would monotonically increase across bins from the initiation of the fixed interval to the end of the trial and thus throughout the interval. For example, for a two-bin analysis, an FI 60 s trial would be divided into two 30 s bins; the contingent response was always placed in the final bin. As response levels are not a form of continuous measurement, we do not include descriptive statistics for these bin analyses.

We performed a series of ordinal analyses to assess if response levels scalloped across the fixed interval by comparing the observed data to a monotonically increasing ordinal prediction. To further assess the response patterns of our observed data, we also performed ordinal assessments opposite of what would be expected if subject responding came under temporal control (i.e., we also predicted a monotonic decrease across bins). We assessed this monotonic decreasing pattern to assess if subjects emitted break-through response (i.e., a series of minor extinction bursts) and to compare multiple ordinal predictions to determine which pattern better characterizes the observed data. Finally, we also predicted each bin would contain an equal number of responses for the two and four bin analyses.

In order to compare individual response rates between the bins within each interval, we used Observation Oriented Modeling (OOM) to compute an observed percent correct classification (PCC) value between our observed data and a 2-, 4-, 10-, or 20-order a priori prediction. For this response bin analysis, we only analyzed the final fixed interval session for individuals; we also pooled data between individuals for our ordinal assessment for group assessments to compare how actual individual performances compare against an abstraction of these performances to identify if this abstraction created a group artifact. Table 2 displays each ordinal assessment's PCC value, randomization range, and *c*-value for the final fixed interval session for each individual subject and group. To assist the interpretability of Table 2, the best fits for each series of ordinal predictions for each individual and group are in bold to indicate which ordinal prediction was best matched by the observed data for each series of analyses when considering PCC, CPCC, and *c*-values. We summarize the main findings of the analyses that are reported in Table 2 in the following section.

**Table 2**  
*Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed	Minimum	Maximum	c-value
			PCC Value	Randomization	Randomization	
	Bee 2	1=2	0.00	0.00	0.00	1.00
		1>2	0.00	0.00	100.00	1.00
		<b>1&lt;2</b>	<b>100.00</b>	<b>0.00</b>	<b>100.00</b>	<b>0.03</b>
	Bee 3	1=2	0.00	0.00	0.00	1.00
		<b>1&gt;2</b>	<b>60.00</b>	<b>0.00</b>	<b>100.00</b>	<b>0.38</b>
		1<2	40.00	0.00	100.00	0.84
	Bee 5	1=2	50.00	50.00	50.00	1.00
		1>2	0.00	0.00	50.00	1.00
		<b>1&lt;2</b>	<b>50.00</b>	<b>0.00</b>	<b>50.00</b>	<b>0.12</b>
	Bee 6	<b>1=2</b>	<b>50.00</b>	<b>50.00</b>	<b>50.00</b>	<b>1.00</b>
		1>2	20.00	0.00	50.00	0.80
		1<2	30.00	0.00	50.00	0.50
0-15	Bee 7	1=2	33.33	33.33	33.33	1.00
		1>2	0.00	0.00	66.67	1.00
		<b>1&lt;2</b>	<b>66.67</b>	<b>0.00</b>	<b>66.67</b>	<b>0.02</b>
	Bee 8	<b>1=2</b>	<b>66.67</b>	<b>66.67</b>	<b>66.67</b>	<b>1.00</b>
		1>2	12.50	0.00	75.00	0.99
		1<2	33.33	0.00	33.33	0.12
	Bee 9	1=2	42.86	42.86	42.86	1.00
		1>2	14.29	0.00	57.14	0.94
		<b>1&lt;2</b>	<b>42.86</b>	<b>0.00</b>	<b>57.14</b>	<b>0.31</b>
	Bee 10	1=2	25.00	25.00	25.00	1.00
		1>2	25.00	0.00	75.00	0.90
		<b>1&lt;2</b>	<b>50.00</b>	<b>0.00</b>	<b>75.00</b>	<b>0.36</b>
	All	1=2	32.26	32.26	32.26	1.00
		1>2	17.74	16.13	51.61	1.00
		<b>1&lt;2</b>	<b>50.00</b>	<b>19.35</b>	<b>48.39</b>	<b>0.01</b>
	Bee 1	1=2	37.50	37.50	37.50	1.00
		1>2	12.50	0.00	62.50	0.96
		1<2	50.00	0.00	62.50	0.19
0-30	Bee 2	1=2	14.29	14.29	14.29	1.00
		1>2	0.00	0.00	85.71	1.00
		<b>1&lt;2</b>	<b>85.71</b>	<b>0.00</b>	<b>85.71</b>	<b>0.02</b>
	Bee 7	1=2	14.29	14.29	14.29	1.00
		1>2	28.57	0.00	85.71	0.89
		1<2	57.14	0.00	85.71	0.35

**Table 2 (cont.)***Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1=2	0.00	0.00	0.00	1.00
	Bee 8	1>2	0.00	0.00	100	1.00
		1<2	<b>100.00</b>	<b>0.00</b>	<b>100</b>	<b>0.01</b>
		1=2	9.09	9.09	9.09	1.00
0-30	Bee 9	1>2	9.09	9.09	9.09	1.00
		1<2	<b>81.82</b>	<b>0.00</b>	<b>90.91</b>	<b>0.01</b>
		1=2	15.38	15.38	15.38	1.00
	All	1>2	10.26	20.51	69.23	1.00
		1<2	<b>74.36</b>	<b>17.95</b>	<b>69.23</b>	<b>0.01</b>
		1=2=3=4	30.00	30.00	30.00	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	13.33	6.67	60.00	0.99
	Bee 2	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>56.67</b>	<b>3.33</b>	<b>63.33</b>	<b>0.01</b>
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	18.33	18.33	18.33	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		<b>1&gt;2&gt;3&gt;4</b>	<b>41.67</b>	<b>18.33</b>	<b>61.67</b>	<b>0.49</b>
	Bee 3	Complete 1>2>3>4	0.00	0.00	20.00	1.00
		1<2<3<4	40.00	23.33	63.33	0.59
0-15		Complete 1<2<3<4	0.00	0.00	20.00	1.00
		1=2=3=4	41.67	41.67	41.67	1.00
		Complete 1=2=3=4	16.67	16.67	16.67	1.00
		1>2>3>4	11.11	5.56	52.78	0.99
	Bee 5	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>47.22</b>	<b>8.33</b>	<b>52.78</b>	<b>0.03</b>
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		<b>1=2=3=4</b>	<b>52.08</b>	<b>52.08</b>	<b>52.08</b>	<b>1.00</b>
		Complete 1=2=3=4	25.00	25.00	25.00	1.00
		1>2>3>4	22.92	4.17	41.67	0.62
	Bee 6	Complete 1>2>3>4	0.00	0.00	0.00	1.00

1<2<3<4	25.00	4.17	43.75	0.51
Complete 1<2<3<4	0.00	0.00	0.00	1.00

**Table 2 (cont.)**  
*Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1=2=3=4	44.44	44.44	44.44	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	9.26	5.56	46.30	1.00
	Bee 7	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>46.30</b>	<b>7.41</b>	<b>46.30</b>	<b>0.01</b>
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	31.48	31.48	31.48	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	18.52	14.81	55.56	0.99
	Bee 8	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>50.00</b>	<b>9.26</b>	<b>55.56</b>	<b>0.02</b>
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	35.71	35.71	35.71	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
0-15		1>2>3>4	19.05	0.00	54.76	0.98
	Bee 9	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>45.24</b>	<b>4.76</b>	<b>57.14</b>	<b>0.08</b>
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	20.83	20.83	20.83	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	27.08	14.58	62.50	0.96
	Bee 10	Complete 1>2>3>4	0.00	0.00	12.50	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>52.08</b>	<b>16.67</b>	<b>64.58</b>	<b>0.09</b>
		Complete 1<2<3<4	0.00	0.00	12.50	1.00
		1=2=3=4	33.87	33.87	33.87	1.00
		Complete 1=2=3=4	4.84	4.84	4.84	1.00
		1>2>3>4	21.51	25.00	41.13	1.00
	All	Complete 1>2>3>4	0.00	0.00	3.23	1.00
		<b>1&lt;2&lt;3&lt;4</b>	<b>44.62</b>	<b>26.34</b>	<b>42.47</b>	<b>0.01</b>

		Complete 1<2<3<4	0.00	0.00	3.23	1.00
		1=2=3=4	33.33	33.33	33.33	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	22.92	10.42	56.25	0.94
0-30	Bee 1	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		1<2<3<4	43.75	10.42	56.25	0.11
		Complete 1<2<3<4	0.00	0.00	0.00	1.00

**Table 2 (cont.)***Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1=2=3=4	23.81	23.81	23.81	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	11.90	14.29	61.90	1.00
	Bee 2	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		1<2<3<4	64.29	11.90	66.67	0.02
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	16.67	16.67	16.67	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
		1>2>3>4	28.57	14.29	71.43	0.94
	Bee 7	Complete 1>2>3>4	0.00	0.00	28.57	1.00
		1<2<3<4	54.76	14.29	66.67	0.10
		Complete 1<2<3<4	14.29	0.00	28.57	0.12
		1=2=3=4	33.33	33.33	33.33	1.00
		Complete 1=2=3=4	0.00	0.00	0.00	1.00
0-30		1>2>3>4	2.78	8.33	58.33	1.00
	Bee 8	Complete 1>2>3>4	0.00	0.00	0.00	1.00
		1<2<3<4	63.89	5.56	61.11	0.01
		Complete 1<2<3<4	0.00	0.00	0.00	1.00
		1=2=3=4	22.73	22.73	22.73	1.00
		Complete 1=2=3=4	9.09	9.09	9.09	1.00
		1>2>3>4	15.15	16.67	57.58	1.00
	Bee 9	Complete 1>2>3>4	0.00	0.00	27.27	1.00
		1<2<3<4	62.12	18.18	60.61	0.01
		Complete 1<2<3<4	0.00	0.00	18.18	1.00
		1=2=3=4	25.64	25.64	25.64	1.00
		Complete 1=2=3=4	2.56	2.56	2.56	1.00
		1>2>3>4	16.67	26.07	48.29	1.00
	All	Complete 1>2>3>4	0.00	0.00	7.69	1.00
		1<2<3<4	57.69	25.21	48.29	0.01
		Complete 1<2<3<4	2.56	0.00	7.69	0.22

0-15	Bee 2	1>...>10	14.22	10.67	38.22	0.99
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 3	1<...<10	<b>33.33</b>	<b>12.00</b>	<b>36.89</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 2	1>...>10	35.33	23.33	45.33	0.46
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 3	1<...<10	34.67	23.11	44.44	0.58
		Complete 1<...<10	0.00	0.00	0.00	1.00

**Table 2 (cont.)**  
*Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
0-15	Bee 5	1>...>10	11.48	9.26	34.07	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 6	1<...<10	<b>30.74</b>	<b>10.00</b>	<b>33.33</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 6	1>...>10	26.94	17.78	39.72	0.60
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 7	1<...<10	28.89	13.61	40.28	0.40
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 7	1>...>10	6.91	7.65	24.94	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 8	1<...<10	<b>24.69</b>	<b>6.42</b>	<b>25.19</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 8	1>...>10	12.35	11.60	28.64	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 9	1<...<10	<b>28.40</b>	<b>9.63</b>	<b>28.89</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 9	1>...>10	15.24	11.43	33.97	0.98
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 10	1<...<10	<b>29.21</b>	<b>11.11</b>	<b>32.06</b>	<b>0.03</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-15	Bee 10	1>...>10	24.17	21.67	44.19	0.99
		Complete 1>...>10	0.00	0.00	0.00	1.00

		>10				
	Bee 10	1<...<10	<b>40.83</b>	<b>18.33</b>	<b>47.5</b>	<b>0.02</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>10	19.07	21.40	29.25	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	All	1<...<10	<b>31.25</b>	<b>21.15</b>	<b>30.47</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>10	20.00	12.50	35.00	0.87
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 1	1<...<10	27.78	13.06	33.89	0.13
0-30		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>10	11.43	11.43	32.70	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 2	1<...<10	<b>32.38</b>	<b>10.48</b>	<b>32.70</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00

**Table 2 (cont.)***Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1>...>10	26.67	25.40	51.43	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 7	1<...<10	<b>46.98</b>	<b>23.49</b>	<b>51.43</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>10	1.85	6.67	26.30	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 8	1<...<10	<b>30.00</b>	<b>5.93</b>	<b>25.93</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
0-30		1>...>10	18.59	25.86	44.65	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	Bee 9	1<...<10	<b>51.72</b>	<b>23.64</b>	<b>44.44</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>10	16.47	22.85	32.82	1.00
		Complete 1>...>10	0.00	0.00	0.00	1.00
	All	1<...<10	<b>39.15</b>	<b>21.88</b>	<b>33.11</b>	<b>0.01</b>
		Complete 1<...<10	0.00	0.00	0.00	1.00
		1>...>20	8.53	6.84	20.74	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 2	1<...<20	<b>19.68</b>	<b>7.47</b>	<b>21.16</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	26.58	18.89	32.16	0.32
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 3	1<...<20	24.79	18.63	31.74	0.66
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	7.11	6.49	17.46	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
0-15	Bee 5	1<...<20	<b>16.93</b>	<b>6.40</b>	<b>17.89</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	19.14	12.37	25.53	0.47
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 6	1<...<20	18.95	11.91	25.46	0.52

	Complete 1<...<20	0.00	0.00	0.00	1.00
	1>...>20	3.98	3.68	12.46	1.00
	Complete 1>...>20	0.00	0.00	0.00	1.00
Bee 7	1<...<20	<b>12.87</b>	<b>4.50</b>	<b>12.22</b>	<b>0.01</b>
	Complete 1<...<20	0.00	0.00	0.00	1.00

**Table 2 (cont.)***Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1>...>20	7.60	6.67	16.67	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 8	1<...<20	<b>15.50</b>	<b>7.25</b>	<b>16.55</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	9.32	7.14	18.72	.97
		Complete 1>...>20	0.00	0.00	0.00	1.00
0-15	Bee 9	1<...<20	<b>16.24</b>	<b>6.09</b>	<b>18.42</b>	<b>0.03</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	18.49	15.72	31.64	.98
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 10	1<...<20	<b>27.37</b>	<b>15.86</b>	<b>29.74</b>	<b>0.02</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	13.25	13.67	18.18	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
	All	1<...<20	<b>19.15</b>	<b>14.32</b>	<b>18.29</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	13.09	8.36	21.18	0.80
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 1	1<...<20	15.72	7.70	19.80	0.26
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	7.37	7.22	19.17	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 2	1<...<20	<b>19.10</b>	<b>6.24</b>	<b>18.5</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	20.68	19.70	37.97	1.00
0-30		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 7	1<...<20	<b>38.65</b>	<b>19.32</b>	<b>38.27</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00
		1>...>20	1.58	4.39	15.18	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
	Bee 8	1<...<20	<b>18.33</b>	<b>3.95</b>	<b>15.61</b>	<b>0.01</b>

	Complete 1<...<20	0.00	0.00	0.00	1.00
	1>...>20	16.32	20.86	35.31	1.00
	Complete 1>...>20	0.00	0.00	0.00	1.00
Bee 9	1<...<20	<b>39.14</b>	<b>20.77</b>	<b>34.31</b>	<b>0.01</b>
	Complete 1<...<20	0.00	0.00	0.00	1.00

**Table 2 (cont.)***Honey bee response bin OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
		1>...>20	12.56	17.11	22.93	1.00
		Complete 1>...>20	0.00	0.00	0.00	1.00
0-30	All	1<...<20	<b>27.45</b>	<b>16.87</b>	<b>22.60</b>	<b>0.01</b>
		Complete 1<...<20	0.00	0.00	0.00	1.00

Honey bee responding did not tend to follow a monotonically increasing ordinal pattern which is taken to indicate responding was temporally controlled. Of the three ordinal predictions that were made for the two-bin analysis ( $1=2$ ;  $1>2$ ;  $1<2$ ), most honey bee subjects best matched the prediction that more responses were emitted at the end of the fixed interval. However, no individual subjects produced PCC values for the monotonically increasing ordinal prediction that were larger than the maximum randomization range PCC value. Thus, many observed PCC values did not differ from the randomization range for the two-bin assessment, which does not clearly support a conclusion, that responding came under temporal control. Interestingly, a PCC value of 50.00 was observed when pooling all 0-15 subjects' response data while the pooled 0-30 group produced a PCC value of 74.36; these were the only two bin assessments that produced PCC values that were larger than the maximum randomization range PCC value; however, the difference between these maximum randomization ranges (48.39 and 69.23, respectively) does not widely differ from the observed PCC values. Thus, responding was not clearly observed to be monotonically increasing for the two bin analysis for individual honey bee subjects, and only the pooled shorter FI 30 s schedule seemed to match the prediction taken to indicate responding was temporally controlled.

For the four-bin analysis, honey bees did not clearly match a monotonically increasing ordinal prediction ( $1<2<3<4$ ) that would have indicated responding scalloped. The PCC values for this ordinal pattern ranged from 25.00 to 64.29 for the 2-order comparisons. While some of these PCC values may seem large, it is important to note that the CPCC values for these 4-order assessments were very low for the honey bee subjects; all CPCC values were zero for individual subjects other than for B7 (0-30), which produced a CPCC value of only 14.29. The more conservative CPCC value assesses if the entire trial follows the ordinal prediction (i.e.,  $1<2<3<4$ ) whereas the less conservative PCC value makes pair-wise assessments (i.e.,  $1<2$ ,  $1<3$ ,  $1<4$ ,  $2<3$ ,  $2<4$ ,  $3<4$ ). Thus, while the PCC values may seem impressive for these ordinal predictions, these subjects did not emit scalloped predicted patterns within trials because of the low observed CPCC values. A four-bin analysis of responses that are temporally controlled should produce CPCC values above what was observed for these honey bee subjects. The reason these PCC values are high is likely due to the pair-wise comparisons involving the final bins; the steady-state response record prediction ( $1=2=3=4$ ) contained PCC values as high as 52.08. Thus, the CPCC values were low because the first two or three bins were equal in several cases. However, pooled groups did match the monotonically increasing ordinal prediction and produced PCC

values that were larger than the maximum randomization range PCC values, which supports a conclusion of temporal control at the group level.

For the 10 bin analysis, most honey bees did not clearly match a monotonically increasing ordinal prediction ( $1 < \dots < 10$ ); only Subjects B8 and B9 (0-30) produced PCC values that were larger than the maximum randomization range PCC value. Individuals in the 0-15 group produced PCC values ranging from 24.69 to 40.83 while the individuals in the 0-30 group produced PCC values ranging from 27.78 to 51.72. The CPCC values for all subjects were zero, and the randomization ranges do not produce CPCC values over zero; a complete pattern match is a very strict assessment for these data. Thus, only two of 13 individual subjects clearly produced monotonically increasing response levels for the 10-bin analysis. Additionally, pooled groups did match the monotonically increasing ordinal prediction and produced PCC values that were larger than the maximum randomization range PCC values.

For the 20 bin analysis, most honey bees did not clearly match a monotonically increasing ordinal prediction ( $1 < \dots < 20$ ); only five of 13 subjects produced PCC values that were larger than the maximum randomization range PCC values. Individuals in the 0-15 group produced PCC values ranging from 12.87 to 24.79 while individuals in the 0-30 group produced PCC values ranging from 15.72 to 39.14. Again, while the CPCC values for all subjects were zero, the randomization ranges do not produce CPCC values over zero; a complete pattern match is a very strict assessment for these data. Finally, pooled groups did match the monotonically increasing ordinal prediction and produced PCC values that were larger than the maximum randomization range PCC values.

Taken together, honey bee subjects' performances varied between individuals and produced inconsistent evidence of temporal control; however, most subjects did not produce PCC values that were larger than the maximum randomization range. Thus, at an individual level, most honey bees did not produce scalloped response patterns and did not produce scalloped response patterns when considering individual trials as all CPCC values were low. Interestingly, pooling the subjects into their respective groups did produce PCC values that were larger than the maximum randomization ranges; thus, we observed a group artifact that does not truly represent the individuals, or their trials. We interpret our pooled group performances as an artifact for two reasons. First, the pooled group performance effect was stronger than the individual subjects' performance; second, the pooled group performance does not exist in reality, for only the direct observations of the individuals' performances actually occurred. We observed individuals with weak patterns in reality; stronger pooled patterns do not represent the individuals or reality. This is not to say all pooling procedure inherently create artifacts; pooled group patterns, while not existing in reality, still can represent individuals without altering the patterns of the individual subjects; however, we observed the aggregate effect did not truly represent the individual, real observations.

## **Quarter Life Analysis**

Quarter life is defined as the interval of time in which the first quarter of total responses made during the fixed interval occurs (Herrnstein & Morse, 1957). If fewer than four responses were emitted by the subject within a trial, we did not include that trial in our quarter life assessments as quarter life requires at least four responses to be calculated. We also did not include the first trial of each session, which was a single

response trial to initiate the fixed interval for the second trial. As quarter life is a truly continuous measure (i.e., time), we present descriptive statistics of subject quarter lives for the final fixed interval session in Table 3; a clear increase in average quarter life across longer fixed interval schedules is not readily observable for the honey bee subjects. Average quarter lives, when considering all final session ranged between 6.88% and 47.60% of the fixed interval for individual subjects. The pooled FI 15 s schedule average quarter life occurred at 21.50% of the fixed interval while the pooled FI 30 s schedule average quarter life occurred at 31.87% of the fixed interval. Compared to vertebrates, which can produce quarter lives occurring as late as 75.00% of the fixed interval (e.g., Herrnstein & Morse, 1957), these honey bees did not produce large summary statistics for quarter life.

To assess differences in honey bee quarter lives between fixed interval schedule durations, we only performed a single two-way ordinal assessment between the FI 15 s condition and FI 30 s condition. For subjects that completed the experiment in the 0-15 and 0-30 groups, each group’s final session’s trials were compared under the prediction that longer fixed interval schedule durations would produce longer quarter lives. When comparing quarter lives of the 0-15 and 0-30 groups, larger quarter lives were observed for the 0-30 group compared to the 0-15 group (PCC value: 81.14; randomization range: 42.86-56.14; c-value < 0.01). From this assessment, a clear relative schedule effect is observable for the honey bees; again, the quarter life values produced by individual and pooled subjects were low compared to vertebrate performances (e.g., Herrnstein & Morse, 1957).

**Table 3**  
*Quarter life descriptive statistics*

Group	Subject	<i>M</i> (s)	<i>M</i> % of Fixed Interval	<i>Mdn</i> (s)	<i>Mdn</i> % of Fixed Interval	<i>SD</i>
0-15	Bee 2	7.14	47.60	7.14	47.60	*
	Bee 3	3.64	24.27	2.63	17.55	2.20
	Bee 5	*	*	*	*	*
	Bee 6	1.03	6.88	0.84	5.57	0.40
	Bee 7	*	*	*	*	*
	Bee 8	2.95	19.63	2.28	15.21	0.94
	Bee 9	3.91	26.04	3.91	26.04	*
	Bee 10	4.17	27.80	1.84	12.29	3.87
	All	3.22	21.50	2.22	14.79	2.75
	0-30	Bee 1	5.73	19.10	1.33	4.42
Bee 2		5.06	16.87	2.90	9.67	3.20
Bee 7		11.22	37.39	7.57	25.24	6.06
Bee 8		*	*	*	*	*
Bee 9		12.40	41.34	12.11	40.37	4.03
All		9.56	31.87	8.69	28.96	6.10

*Note: An asterisk denote too few responses were made to calculate quarter life descriptive statistics*

## Post-reinforcement Pause Analysis

Longer post-reinforcement pauses have been traditionally (e.g., Schneider, 1969) observed to occur with longer FI schedule durations. As post-reinforcement pause (PRP) is a truly continuous measure (i.e., time), Table 4 presents PRP descriptive statistics for each individual's and group's final CRF and FI sessions. A clear increase in average PRP when comparing the final CRF and FI sessions was observed for most subjects; only B6 and B9 from the 0-15 group did not produce an increase in PRP when comparing the final CRF versus FI sessions. Medians indicated fewer individual subjects in the 0-15 group followed this trend; Subjects 3, 6, 9 and 10 (0-15) did not emit longer median PRPs when comparing the final CRF vs. FI sessions. However, all 0-30 subjects increased in median PRP when responding was reinforced on fixed interval schedules. The final FI session also tended to produce higher standard deviations in latency or PRP compared to the final CRF session for most honey bees. We also present the percentage into the fixed interval when the average first response is made for honey bees in Table 4. These percentages were highly variable for the honey bee subjects (ranging from 0.25% to 85.99% of the fixed interval).

We used two strategies to perform an individual analysis of honey bee PRPs. First, two-way ordinal comparisons were made between combinations of the final CRF session and final FI session under the prediction PRPs would be longer during the final FI session compared to the final CRF session. For this prediction, we assessed individual subjects' sessions and also pooled a group's individuals to perform group assessments. The results of these assessments are presented in Table 5; analyses printed in bold did not match the ordinal prediction. Second, a two-way ordinal comparison was made between group schedule durations under the prediction longer fixed interval durations would contain longer PRPs.

**Table 4**  
*Post-reinforcement pause descriptive statistics*

Group	Subject	M (s)	Mdn	SD Final CRF	M (s) Final FI	M % of FI	Mdn (s) Final FI	SD Final FI
		Final CRF	(s) Final CRF					
0-15	Bee 2	1.42	0.42	2.73	4.09	27.29	3.95	1.08
	Bee 3	0.27	0.26	0.11	0.30	2.00	0.24	0.16
	Bee 5	0.80	0.42	0.92	6.04	40.25	6.78	4.02
	Bee 6	1.89	0.48	2.37	0.75	5.01	0.39	1.19
	Bee 7	3.27	3.38	1.93	9.20	61.35	9.49	4.51
	Bee 8	5.55	5.64	2.00	6.19	41.28	6.46	3.59
	Bee 9	4.16	4.02	1.09	3.78	25.18	3.88	0.87
	Bee 10	0.31	0.28	0.14	1.91	12.76	0.27	3.21
	All	1.91	0.42	2.34	3.81	25.40	3.23	3.98
	0-30	Bee 1	1.81	0.30	2.45	4.53	15.09	3.10
Bee 2		1.90	1.71	0.61	4.86	16.19	5.02	4.40
Bee 7		0.31	0.30	0.08	3.33	11.09	3.47	2.89
Bee 8		1.16	0.35	2.30	25.80	85.99	24.55	8.91
Bee 9		4.28	2.92	3.17	3.30	11.01	3.05	1.67
All		2.01	1.31	1.55	7.16	23.87	3.68	10.47

**Table 5**  
*Post-reinforcement pause CRF versus FI OOM ordinal analysis*

Group	Subject	Ordinal Assessment	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
0-15	Bee 2	Final CRF < Final FI	85.71	22.86	74.29	0.01
	Bee 3		<b>51.25</b>	<b>27.5</b>	<b>68.75</b>	<b>0.41</b>
	Bee 5		88.89	26.67	73.33	0.01
	Bee 6		<b>29.69</b>	<b>28.13</b>	<b>71.88</b>	<b>1.00</b>
	Bee 7		89.58	25.00	70.83	0.01
	Bee 8		<b>56.25</b>	<b>31.25</b>	<b>73.44</b>	<b>0.20</b>
	Bee 9		<b>48.21</b>	<b>26.79</b>	<b>73.21</b>	<b>0.67</b>
	Bee 10		<b>51.39</b>	<b>29.17</b>	<b>65.28</b>	<b>0.26</b>
	All		63.76	46.91	51.78	0.01
	0-30		Bee 1	Final CRF < Final FI	71.11	32.22
Bee 2		64.29	26.79		67.86	0.01
Bee 7		98.41	28.57		68.25	0.01
Bee 8		100.00	22.92		79.17	0.01
Bee 9		<b>42.15</b>	<b>35.54</b>		<b>64.46</b>	<b>0.96</b>
All		73.88	45.80		53.55	0.01

Individual honey bee subjects produced inconsistent results when comparing the final FI session compared to the final CRF session; PCC values ranged from 29.69-100.00, so a high degree of variability was observed. The 0-15 group had three of eight subjects that matched the ordinal prediction that the final FI session contained longer

PRPs compared to the final CRF session while the 0-30 group had four of five subjects that matched the ordinal prediction. However, both pooled groups did match the ordinal prediction even though some individuals did not fit this prediction; the 0-15 group matched the prediction (PCC value: 63.76, randomization range: 46.91-51.78,  $c$ -value  $< 0.01$ ) as did the 0-30 group (PCC value: 73.88, randomization range: 45.80-53.55,  $c$ -value  $< 0.01$ ). When comparing PRPs between fixed interval schedule durations, honey bees did produce longer PRPs when responding was reinforced on an FI 30 s compared to an FI 15 s (PCC value: 60.85, randomization range: 46.88-52.87,  $c$ -value  $< 0.01$ ).

Simply stated, honey bees produced inconsistent individual results for the PRP comparisons; six of 13 subjects did not have different PRPs when comparing the CRF session with the FI session, but the pooled honey bee group comparison did reveal a trend between PRP duration and schedule duration.

### **Inter-Response Time Analysis**

If positively accelerating response rates (i.e., a scalloped cumulative response pattern) are used to operationalize temporal control, then negatively accelerating inter-response times can be used as a measure of temporal control (Gentry, Weiss, & Laties, 1983). We performed an ordinal analysis of IRTs within individuals' pooled trials under the prediction that temporally controlled responses would yield monotonically decreasing IRTs across the fixed interval. Table 6 displays each individual subject's final FI session's trials' PCC values, randomization range, and  $c$ -values on each fixed interval schedule for the monotonically decreasing ordinal prediction; assessments in bold indicate which subjects matched the ordinal prediction. We also pooled individuals into appropriate groups for a pooled group PCC and  $c$ -value.

**Table 6**  
*Monotonic decrease inter-response time OOM ordinal analysis*

Group	Subject	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
0-15	Bee 2	27.78	11.11	94.44	0.97
	Bee 3	48.02	37.30	59.79	0.64
	Bee 5	26.67	6.67	93.33	0.97
	Bee 6	35.80	27.16	71.60	0.97
	Bee 7	33.33	0.00	100.00	0.91
	Bee 8	14.29	9.52	95.24	1.00
	Bee 9	45.45	13.64	86.36	0.72
	Bee 10	50.60	27.38	66.67	0.43
	All	46.05	41.27	57.63	0.88
0-30	Bee 1	28.95	28.95	75.00	1.00
	Bee 2	37.21	23.26	83.72	0.94
	Bee 7	48.71	38.19	63.65	0.60
	Bee 8	<b>90.00</b>	<b>0.00</b>	<b>100.00</b>	<b>0.03</b>
	Bee 9	<b>53.67</b>	<b>41.24</b>	<b>54.43</b>	<b>0.01</b>
	All	<b>54.58</b>	<b>42.26</b>	<b>57.02</b>	<b>0.03</b>

Only two of the 13 honey bees fit the monotonically decreasing prediction pattern; the majority of honey bee subjects produced low PCC values ranging as low as 14.29. No subjects in the 0-15 group matched the decreasing ordinal prediction pattern and pooling the 0-15 group did not produce a pattern match (PCC value: 46.05, randomization range: 41.27-57.36,  $c$ -value = 0.88). For the 0-30 group, only B8 (PCC value: 90.00, randomization range: 0.00-100.00,  $c$ -value = 0.03) and B9 (PCC value: 53.67, randomization range: 41.24-54.43,  $c$ -value = 0.01) matched the ordinal prediction; pooling all subjects in the 0-30 group produced a pattern match (PCC value: 54.58, randomization range: 42.26-57.02,  $c$ -value = 0.03). However, while relatively low  $c$ -values were observed (compared to a .05 arbitrary *significance* level), no PCC values were larger than the maximum randomization range PCC value.

We performed a second ordinal prediction for both honey bee IRT patterns under the prediction IRTs would monotonically increase throughout the interval. This prediction assessed if responding occurred at higher levels early in the fixed interval and at lower levels later in the fixed interval. Table 7 displays each individual subjects final FI sessions trials' PCC values, randomization range, and  $c$ -values on each fixed interval schedule for the monotonically increasing ordinal prediction; assessments in bold indicate which subjects matched the ordinal prediction. Only three honey bees matched the monotonically increasing IRT ordinal prediction; B6 (PCC value: 64.20, randomization range: 28.40-75.31,  $c$ -value = 0.03) and B8 (PCC value: 85.71, randomization range: 9.52-90.48,  $c$ -value = 0.01) from the 0-15 group matched the pattern while B1 (PCC value: 71.05, randomization range: 28.95-71.37,  $c$ -value = 0.01) from the 0-30 group matched the ordinal prediction. Again, no individual subject PCC values were larger than the maximum randomization range PCC values. An interesting analysis may be to compare PCC values for each prediction to determine whether a monotonically increasing or decreasing was better fit by the observed IRT data; essentially, this comparison asks what ordinal prediction best characterizes the observed data. From this comparison, it is clear that seven of eight 0-15 and two of five

0-30 honey bees emitted IRT patterns that were better characterized by a monotonically increasing pattern.

**Table 7**  
*Monotonic increase inter-response time OOM ordinal analysis*

Group	Subject	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
0-15	Bee 2	72.22	11.11	88.89	0.06
	Bee 3	50.40	37.83	60.05	0.39
	Bee 5	73.33	6.67	100.00	0.08
	Bee 6	<b>64.20</b>	<b>28.40</b>	<b>75.31</b>	<b>0.03</b>
	Bee 7	66.67	0.00	100.00	0.28
	Bee 8	<b>85.71</b>	<b>9.52</b>	<b>90.48</b>	<b>0.01</b>
	Bee 9	54.55	13.64	90.91	0.42
	Bee 10	47.62	32.14	68.45	0.64
	All	52.57	42.37	58.64	0.14
	0-30	Bee 1	<b>71.05</b>	<b>28.95</b>	<b>72.37</b>
Bee 2		62.79	20.93	81.40	0.12
Bee 7		50.55	36.90	63.10	0.41
Bee 8		10.00	10.00	100.00	1.00
Bee 9		41.77	40.65	54.23	0.99
All		44.91	41.55	58.31	0.98

Simply stated, only two honey bees produced monotonically decreasing IRTs across trials, and most honey bees emitted IRT patterns that better fit a monotonically increasing pattern compared to a monotonically decreasing pattern; however, both pattern fits were low for the majority of honey bee subjects. When pooling subjects into appropriate groups, the monotonically decreasing ordinal prediction better characterized honey bee responding, but these PCC values were not larger than the maximum randomization range PCC values.

## Response Duration Analysis

To our knowledge, no assessments of response duration have been published in the comparative temporal control literature; thus, two ordinal predictions were posited and compared to the observed data. If the initiation of a response is what produces reinforcement, then shorter responses as the interval approaches termination would result in a higher likelihood of reinforcement delivery; holding a long response past the interval's completion reduces efficiency as conceptualized by the number of obtained reinforcers per unit of time. Considering that IRTs can contain response durations as response duration is oftentimes not recorded for procedures using traditional responses that are generally very short, we can expect response duration and IRT may follow similar patterns. Thus, temporally controlled responses should occur in higher numbers towards the end of the interval, and should be shorter towards the end of the interval. The first ordinal analysis predicted a monotonic decrease in response duration across the fixed interval while the second ordinal analysis predicted a monotonic increase in response duration across the fixed interval; the second ordinal prediction is consistent with a temporally controlled hypothesis. Table 8 displays each individual's final session's trials' PCC values, randomization range, and *c*-values for the monotonically decreasing ordinal prediction while Table 9 displays results for the monotonically increasing ordinal prediction; assessments in bold fit the ordinal prediction. We also pooled individuals into appropriate groups for a pooled group PCC value and *c*-value.

**Table 8**  
*Monotonic decrease response duration OOM ordinal analysis*

Group	Subject	Observed PCC Value	Minimum Randomization n	Maximum Randomization	<i>c</i> -value
0-15	Bee 2	22.22	16.67	88.89	0.99
	Bee 3	30.42	39.42	59.92	1.00
	Bee 5	40.00	6.67	93.33	0.80
	Bee 6	24.69	22.22	74.07	1.00
	Bee 7	22.22	0.00	100.00	0.98
	Bee 8	9.52	4.76	85.71	1.00
	Bee 9	30.00	5.00	90.00	0.97
	Bee 10	36.31	33.93	70.83	0.99
	All	30.42	41.54	59.10	1.00
	0-30	Bee 1	39.47	27.63	69.74
Bee 2		27.91	20.93	79.07	0.99
Bee 7		43.54	37.64	61.81	0.92
Bee 8		20.00	0.00	100.00	0.99
Bee 9		38.21	37.66	63.45	1.00
All		39.90	41.26	56.59	1.00

No honey bee matched the ordinal prediction that longer response durations would occur earlier in the fixed interval. While honey bees did not fit the monotonically decreasing ordinal prediction for response duration, five of the eight 0-15 subjects and one of five 0-30 subjects fit the monotonically increasing response duration ordinal prediction. Both the 0-15 (PCC value: 68.84, randomization range: 39.61-58.09,

c-value < 0.01) and 0-30 (PCC value: 59.03, randomization range: 40.90-56.73, c-value < 0.01) pooled honey bee groups fit the monotonically increasing response duration ordinal prediction. Thus, honey bees did not fit the monotonically decreasing ordinal prediction, and more honey bees fit the monotonically increasing ordinal prediction for response duration. From these analyses, honey bees clearly did not produce decreasing response durations throughout the interval.

## Trial Duration Analysis

A relatively simple analysis of temporal control is to assess each trial's duration for each subject to determine the amount of time after the reinforcement contingencies had been met before the subject emitted the trial's final response. Ideally, if subject responding came under perfect temporal control, responding would be inhibited for the entire fixed interval, and a single response would be emitted the instant a response would be reinforced. Thus, observing scallops, break-and-runs, increasing response levels, quarter lives, PRPs that are shorter than the fixed interval, decreasing IRTs, and decreasing response durations are all assessments of imperfect timing and are dependent on the subject making more than one response per trial. Obviously, this perfect response pattern occurs rarely under fixed interval schedules, but a focus on the contingent response may be a fruitful endeavor for temporal control researchers. Table 10 presents descriptive statistics of the interval of time between reinforcer availability and reinforcement delivery for each subject's and group's first and last fixed interval schedule trial durations. Many honey bee subjects produced smaller aggregates of trial duration during the final fixed interval trial compared to the first fixed interval trial.

We performed an ordinal analysis of the interval between reinforcer availability and reinforcement delivery within individuals' pooled trials under the prediction that combinations of the first fixed interval session's trials would be longer than combinations of the last fixed interval session's trials. Table 11 displays each individual's final FI session's trials' PCC, randomization range, and *c*-values on each fixed interval schedule; analyses in bold indicate which subjects matched the ordinal prediction. We also pooled individuals into appropriate groups for a pooled group PCC and *c*-value.

**Table 9**  
*Monotonic increase response duration OOM ordinal analysis*

Group	Subject	Observed PCC Value	Minimum Randomization	Maximum Randomization	<i>c</i> -value
0-15	Bee 2	<b>77.78</b>	<b>5.56</b>	<b>94.44</b>	<b>0.04</b>
	Bee 3	<b>68.65</b>	<b>37.83</b>	<b>59.13</b>	<b>0.01</b>
	Bee 5	60.00	6.67	86.67	0.32
	Bee 6	<b>74.07</b>	<b>28.40</b>	<b>72.84</b>	<b>0.01</b>
	Bee 7	77.78	0.00	100.00	0.09
	Bee 8	<b>90.48</b>	<b>9.52</b>	<b>85.71</b>	<b>0.01</b>
	Bee 9	70.00	15.00	90.00	0.10
	Bee 10	<b>63.69</b>	<b>32.74</b>	<b>70.83</b>	<b>0.01</b>
	All	<b>68.84</b>	<b>39.61</b>	<b>58.09</b>	<b>0.01</b>
	0-30	Bee 1	59.21	27.63	73.68
Bee 2		<b>72.09</b>	<b>18.60</b>	<b>76.74</b>	<b>0.01</b>
Bee 7		54.80	36.90	64.94	0.09
Bee 8		80.00	0.00	100.00	0.06
Bee 9		61.10	39.03	60.00	0.01
All		<b>59.03</b>	<b>40.90</b>	<b>56.73</b>	<b>0.01</b>

**Table 10**  
*Trial duration (seconds) descriptive statistics*

Group	Subject	First FI Session <i>M</i>	First FI Session <i>Mdn</i>	First FI Session <i>SD</i>	Last FI Session <i>M</i>	Last FI Session <i>Mdn</i>	Last FI Session <i>SD</i>
0-15	Bee 2	4.58	3.92	4.01	5.63	4.38	4.26
	Bee 3	2.93	0.70	4.02	1.08	0.63	0.97
	Bee 5	20.13	5.55	24.21	12.76	5.94	18.58
	Bee 6	6.94	5.61	6.92	1.34	1.70	0.84
	Bee 7	5.48	3.77	6.07	6.50	6.54	4.38
	Bee 8	4.76	4.02	4.67	4.81	4.21	3.89
	Bee 9	6.30	3.99	7.19	2.82	1.36	3.70
	Bee 10	3.82	0.58	6.15	1.53	1.30	1.68
	All	5.61	2.47	8.62	4.13	2.13	6.61
0-30	Bee 1	12.50	15.22	8.40	9.37	9.28	6.92
	Bee 2	7.45	6.65	4.85	9.11	5.60	8.87
	Bee 7	19.77	1.38	38.33	5.30	2.09	6.60
	Bee 8	18.71	7.11	23.76	4.77	4.21	4.25
	Bee 9	19.32	14.42	15.84	1.34	1.10	1.25
	All	17.88	7.83	26.29	5.63	2.86	6.38

**Table 11**  
*Trial duration OOM ordinal analysis*

Group	Subject	Observed PCC Value	Minimum Randomization	Maximum Randomization	c-value
0-15	Bee 2	36.67	23.33	76.67	0.94
	Bee 3	53.97	31.75	69.84	0.33
	Bee 5	52.00	20.00	84.00	0.51
	Bee 6	<b>76.19</b>	<b>26.19</b>	<b>76.19</b>	<b>0.01</b>
	Bee 7	37.50	30.56	66.67	0.98
	Bee 8	47.22	33.33	70.83	0.72
	Bee 9	<b>72.22</b>	<b>22.22</b>	<b>83.33</b>	<b>0.01</b>
	Bee 10	48.21	30.36	67.86	0.67
	All	<b>53.56</b>	<b>47.44</b>	<b>52.48</b>	<b>0.01</b>
0-30	Bee 1	<b>60.49</b>	<b>32.10</b>	<b>67.90</b>	<b>0.04</b>
	Bee 2	46.67	26.67	80.00	0.71
	Bee 7	52.38	21.43	73.81	0.45
	Bee 8	<b>73.81</b>	<b>26.19</b>	<b>73.81</b>	<b>0.01</b>
	Bee 9	<b>100.00</b>	<b>30.68</b>	<b>65.91</b>	<b>0.01</b>
	All	<b>70.29</b>	<b>46.61</b>	<b>53.12</b>	<b>0.01</b>

Only two of eight 0-15 while three of five 0-30 honey bees matched the ordinal prediction that the final fixed interval session had shorter trials compared to the first fixed interval session. B9 (0-30) produced the most convincing pattern match (PCC value: 100.00, randomization range: 30.68-65.91, c-value < 0.01). The pooled 0-15

group produced a pattern match that did not widely differ from the randomization range (PCC value: 53.56, randomization range: 47.44-52.48,  $c$ -value  $< 0.01$ ) while the 0-30 group produced a clear pattern match that did widely differ from the randomization range (PCC value: 70.29, randomization range: 46.61-53.12,  $c$ -value  $< 0.01$ ). Thus at an individual level, most honey bees did not clearly fit the prediction that longer trial durations would occur during the first FI session compared to the last FI session, but pooling individuals into groups did produce a clear pattern match (especially for the 0-30 group).

## **Discussion**

We assessed multiple measures of honey bee responding when reinforced on two fixed interval schedules to determine if responding was temporally controlled. While no direct species comparisons were performed due to instrumentation differences between the protocols, indirect comparisons reveal the majority of honey bees did not convincingly emit responses that came under temporal control. Our findings confirm Grossmann's (1973) conclusion that honey bee responding does not come under temporal control. Our findings contrast with Bosivert and Sherry's (2006) claim that the performance of bumble bees can come under temporal control. While the divergence in the invertebrate fixed interval literature could be an indication of species differences, without further replication and more extensive analyses of bumble bee responding beyond aggregate analyses, a conclusion of a species difference between honey bees and bumble bees would be premature. Of these analyzed operationalizations of temporal control, no traditional measures supported the conclusion that most honey bee's responding came under temporal control.

## **Cumulative Curves**

Most honey bee cumulative response curves displayed break-through and steady state response patterns while only four of 13 subjects emitted responses for a handful of trials that were interpretable as being temporally controlled. From this traditional, qualitative, and indirect comparison, we observed most honey bees did not emit responses that support a conclusion that responding came under temporal control. The honey bees emitted either a response pattern that mirrors a series of minor extinction bursts, or a response pattern that does not widely differ from responding on a CRF schedule of reinforcement. As we did not observe break-and-run cumulative records, we did not perform break-and-run analyses or assess breakpoint, which is a common measure to assess when responding shifts from low levels to high levels (Schneider, 1969).

Our findings confirm Grossmann's (1973) conclusion that honey bee responding does not come under temporal control on fixed interval schedules despite the difference in the number of training trials between the presently reported sample of honey bees and Grossmann's (1973). It is possible Grossmann (1973) did not observe honey bee responding came under temporal control because the subjects encountered different reinforcement contingencies between sessions (and days). We attempted to avoid this issue, but were obliged to collect data from one day per subject and thus could not expose our subjects to the same number of trials as Grossmann (1973).

## **Response Bins**

At an individual level, we did not observe the honey bee subjects emitted monotonically increasing ordinal predictions for the 2-, 4-, 10-, and 20-bin analyses. However, when pooling subjects into appropriate groups, we did observe response levels seemed to monotonically increase across the fixed interval; this finding confirms Bosivert and Sherry's (2006) modified bin analysis which was only conducted at a group, aggregate level. We contend that if individual subjects do not emit monotonically increasing response levels across the fixed intervals, that responding cannot be concluded as having come under temporal control regardless of pooled group performances. Our findings contribute to a rich line of cautioning against the utilization of group and aggregate analyses of fixed interval performances (e.g., Branch & Gollub, 1974; Dews, 1978; Schneider, 1969; Zeiler & Powell, 1994).

An important consideration for the bin analyses is how to divide the bins. Selecting the number of bins is a balance between avoiding having empty bins, but also having a finer resolution of analysis. Beyond simply selecting a number of bins to use (which is an arbitrary decision), several methods of dividing the fixed interval trial to calculate bins exist, and the selection of these methods also appears to be a rather arbitrary decision. Unfortunately, the literature does not explicitly explain how fixed interval bins are created, and multiple methods have likely been utilized and treated as if they are one in the same.

Three binning methods seem to exist in the literature; to describe the differences between these methods, consider a two-bin division of a FI 60 s session with a contingent response that is made 66 s after the initiation of the fixed interval, or six s after the contingency has been met. First, the fixed interval can be divided into truly equal bins, and the final response of the trial (which occurs after the final bin) is not included in the final bin. The first bin would be 30 s while the final bin would be 30 s; it is possible to have two empty bins if responding is inhibited until the completion of the fixed interval with this method. Second, the fixed interval can be divided into equal bins with the exception of the final bin of the trial, which contains the final response of the trial. The first bin would be 30 s while the final bin would be 36 s; with this method, it is impossible to have two empty bins if responding is inhibited until the completion of the fixed interval. This is the method reported here, and it appears to be the most common within the fixed interval literature. Third, rather than the fixed interval, the trial can be divided into equal duration bins. The first bin would be 33 s while the final bin would be 33 s; with this method, it is impossible to have two empty bins if responding is inhibited until the completion of the fixed interval. This is the method reported in Craig et al. (2014); different methods to bin responses were utilized by Craig et al. (2014) and the present manuscript. Clearly, in addition to deciding the appropriate number of bins to divide the fixed interval, researchers must use a standardized method to divide the fixed intervals.

## **Quarter Life**

Honey bee quarter lives typically occurred before or around the first quarter of the fixed interval had elapsed; this finding indicates responding was not uniform and that more responses were emitted towards the beginning of the interval rather than

later in the interval. Based on our quarter life assessment, a clear difference of when quarter lives occurred is observable between schedules; honey bees produced longer quarter lives when responding was reinforced on longer fixed interval schedules, and this assessment could be used to support the conclusion that honey bee responding came under temporal control. Thus, descriptive statistics indicated responding was not clearly temporally controlled while a direct schedule comparison of quarter life indicated responding may have been temporally controlled.

We recommend returning to the quarter life measure for four reasons. First, the measure is continuous (i.e., expressed in time), and common aggregates can be realistically computed for quarter life. Second, the measure is easily calculable and compared. Third, the measure is conceptually easy to understand. Fourth, the measure facilitates easy species comparisons. Our main concern regarding quarter life is that at least four responses must be emitted in order for quarter life to be calculated; perfectly temporally controlled responding (i.e., a single response being emitted the instant the fixed interval elapses) cannot produce quarter lives. For this reason, only relying on quarter life as an assessment of temporal control is unadvisable as stated by Dukich and Lee (1973). Additionally, quarter life is an arbitrary measure, and investigations of half or third life may be beneficial for temporal control researchers.

## **Post-reinforcement Pause**

Boisvert and Sherry (2006) and Craig et al. (2014) both investigated PRP differences between fixed interval schedules. Boisvert and Sherry (2006) concluded bumble bee subjects had longer average PRPs during longer fixed interval conditions; however, individual subjects were not assessed whereas we and Craig et al. (2014) did perform an individual analysis. For the present analyses, clear increases in mean and median PRPs and latencies were observed for most honey bee subjects when comparing the final CRF versus the final fixed interval session.

We performed two PRP comparisons. The first comparison assessed if the final fixed interval session had longer PRPs compared to the final CRF session. Using OOM, we observed the pooled honey bee analyses fit the ordinal prediction, but six of 13 individual subjects did not fit the ordinal prediction. A pooled PRP analysis in honey bees confirmed Boisvert and Sherry's (2006) findings, but nearly half of the individual honey bee subjects did not emit longer PRPs during the fixed interval condition compared to CRF sessions. Thus, the conclusion of temporal control in invertebrates according to PRP may be an artifact of aggregate analyses. Clearly, performing individual analyses is critical for temporal control researchers as learning cannot occur in group representations but can only occur in individuals; we recommend performing individual analyses in addition to group assessments.

The second PRP comparison assessed if longer schedule durations had longer PRPs or latencies compared to shorter schedule durations. These assessments were comprised of between-subject comparisons of pooled groups for the 0-15 and 0-30 subjects. Observation Oriented Modeling revealed honey bee subjects fit the ordinal prediction that longer schedules would contain longer PRPs, but the observed PCC value was close to the maximum randomization range. Thus, honey bees did not convincingly emit longer PRPs during longer fixed interval schedule durations.

We recommend researchers continue to investigate PRP at different schedule durations. This measure is continuous, meaningful, easy to perform, and has been a staple in the temporal control literature for almost half a century. However, simply performing aggregate analyses may not be sufficient to identify if responding came under temporal control; we recommend performing both individual and pooled/aggregate analyses. Finally, because PRP is a highly variable measure (e.g., Powell, 1972), complementing a PRP analysis with other measures that have been taken to indicate temporal control is advisable.

### **Inter-response Time (IRT)**

If a scalloped response pattern is taken to indicate responding came under temporal control, then a decrease in IRTs across the session may be indicative of a scalloped response pattern. Unfortunately, this ordinal prediction can only be an assessment of scalloped response patterns; break-and-run response patterns may not fit this ordinal prediction. However, based on the observed break-through and steady-state cumulative response records for these honey bee subjects, our ordinal IRT analyses are unlikely to be affected by this concern; future fixed interval investigations may need to consider this point.

We performed two ordinal analyses of IRT; we predicted monotonic increases or decreases in IRTs across trials and compared the fit of each subject's final session's pooled trials to either ordinal prediction. Only two honey bee subjects fit the monotonically decreasing ordinal prediction while three honey bee subjects fit the monotonically increasing ordinal prediction; no pooled honey bee analyses fit either ordinal prediction. While only three honey bee subjects fit the monotonically increasing ordinal prediction, nine of the thirteen honey bee subjects' response patterns were better characterized by the monotonically increasing ordinal prediction compared to the monotonically decreasing ordinal prediction. Thus, the majority of honey bees better fit the prediction indicating subjects took longer to emit responses towards the end of the fixed interval; this type of response pattern is the opposite of a scalloped response pattern (i.e., break-through) and does not support the conclusion that honey bee responding came under temporal control.

We only reported pooled trial comparisons for subjects; most individual trials did not fit the ordinal predictions. This finding echoes a similar finding by Gentry, et al. (1983), for only aggregates, not individual trials, fit the same ordinal prediction we made here. As stated previously, this may be due to the fact that the monotonically decreasing IRT assessment creates an assessment of whether the observed response patterns were scalloped; Branch and Gollub (1974) revealed scallops may be an artifact of aggregating break-and-run response patterns.

### **Trial Duration**

If responding came under temporal control, it stands to reason that subjects would emit responses closer to the completion of the fixed interval with extensive exposure to the fixed interval schedule. We observed this effect for some honey bee subjects when assessing mean and median comparisons. We made an ordinal

prediction to perform an individual analysis of trial duration and observed only five of 13 honey bees fit this ordinal prediction. Hence, this assessment of temporal control indicates a minority of the honey bee subjects may have emitted temporally controlled responses.

We maintain that an assessment of the temporal location of the contingent response is necessary for an analysis of temporal control, and if a contingent response occurs well after the fixed interval, responding has not accurately come under temporal control. Obviously, the nuances of temporally controlled responding is not assessed via this measure but satisfying this measure is critical in order for responding to be considered as having come under temporal control. Hence, we recommend trial duration be used in conjunction with other measures for this reason. One glaring issue with a trial duration assessment is that instrumentation differences between assessed species may greatly influence this measure; a full body poke may be easier to emit, and be emitted more quickly, compared to a more difficult response such as hoop-swimming behavior (e.g., Higa & Simm, 2004). Thus, using trial duration to directly compare responding across different species does not seem to be a fruitful assessment, but indirect comparisons may still be useful.

## **Response Duration**

No previous fixed interval investigations have assessed how response durations change across the fixed interval, so we performed two ordinal predictions; response durations were predicted to monotonically increase or decrease across the fixed interval. We posit that temporally controlled responses should be shorter as the fixed interval nears completion, for the initiation of a response can only produce reinforcement delivery; a long response directly preceding the completion of the fixed interval decreases reinforcement likelihood. Increasing response durations as the interval progresses reduces reinforcement likelihood as the initiation of a contingent response produces reinforcement delivery.

No honey bees decreased their response durations across the interval. In contrast, six of thirteen honey bees fit the monotonically increasing ordinal prediction. From this assessment, we can conclude honey bees tended not to emit monotonically decreasing response durations across the interval; thus, an inference that honey bee responding came under temporal control is not supported. Increasing response durations throughout the fixed interval reduce the likelihood of making a response once reinforcement is available. For this reason, increasing response durations can be taken to indicate responding is not temporally controlled. Future temporal control assessments may benefit from assessing if the observed response durations are better characterized by a monotonically increasing or decreasing response pattern. Additionally, to assess the relation between response duration and temporal control, allowing the contingency to be met while a response is being made may be beneficial.

## **Future Directions**

Future fixed interval investigations may benefit from addressing the inconsistently utilized measures that have been used to operationalize temporal control. Zeiler and Powell (1994) attempted to isolate a handful of measures (using response

bins, PRP, breakpoint, and peak procedures) to operationalize temporal control; however, we recommend using a greater variety of measures to operationalize temporal control for two reasons. First, if IRT and response duration are recorded, all of the previously described measures can easily be constructed post hoc. Second, several measures (e.g., PRP, quarter life, break point, trial duration) do not describe responding throughout the entire interval; multiple measures must be addressed to fully describe temporally controlled behavior. In our view, returning to a within-trial analysis of IRT is critical and developing methods to assess break-and-run IRT response patterns seems likely to be a worthwhile endeavor. Echoing the concerns outlined by Branch and Gollub (1974), we believe researchers must consider the importance of focusing on individual observations, and we have outlined a series of viable individual analyses to keep the researcher close to the actual observations rather than chasing population parameters.

For future comparative fixed interval investigations, we recommend focusing on a greater diversity of species as per Richelle and Lejeune's (1980, 1984) first recommended strategy. No amphibians have been investigated, and only a handful of fish and reptiles have been assessed (and the majority of species investigations have not been replicated). Specifically, we recommend focusing on aquatic invertebrate species and investigating a rather general hoop-swimming response that most species can likely emit. For example, we are interested in assessing if hoop-swimming in cuttlefish and octopi can be brought under temporal control and comparing these response patterns with those of turtles and fish. This line of research echoes Richelle and Lejeune's (1980, 1984) second recommended strategy of investigating closely related species to reduce instrumentation differences in between-species comparisons. An added benefit of working with aquatic species is that small amounts of experimenter oversight are required. This factor could facilitate a higher number of fixed interval trials and sessions being administered for aquatic species; we were limited to only collecting data from a single day per subject because we could not control what contingencies subjects would encounter between days. It is possible honey bees require a higher number of FI trials for their responses to come under temporal control than reported here; this is part of the difficulty of working with wild and unconfined species. However, it is important to note that while Grossmann (1973) assessed responding over multiple days and administered more trials than reported here, Grossmann (1973) still did not observe honey bees emitted temporally controlled responding. Finally, continuing to investigate a greater variety of terrestrial invertebrates is an important line of research; only bees have been investigated, and the high levels of individual variation in this sample of honey bee response patterns stifles general claims about invertebrates' ability to emit temporally controlled responses. We recommend investigating a wider range of insects, and also recommend performing arachnid investigations.

As per Richelle and Lejeune's (1980, 1984) third recommended strategy, we believe temporal control researchers would benefit from considering several important instrumentation concerns. Specifically, a wider range of responses can be measured by using responses that break infrared beams. The invertebrate fixed interval literature utilizes responses involving breaking infrared beams similarly to responses used with lower order vertebrate species (e.g., Higa and Simm's (2004) responses with Siamese fighting fish). This type of response may be better suited for a wider range of species compared to traditional lever- and key-presses, and can be used for aquatic or terrestrial species, and we recommend utilizing this type of response for future comparative investigations.

Additionally, we recommend utilizing a wide range of reinforcers. For example, Place, Varnon, Craig, and Abramson (in press) trained rattlesnakes to make lever presses in order to receive changes in temperature; we plan to continue working with a similar protocol using spatial responses and exposing rattlesnake responding to fixed interval schedules in the future. Manipulating temperature for ectotherms is not a novel method within the fixed interval literature (Rozin, 1965), but temperature changes have not been used as the primary reinforcement for any fixed interval investigations. This may be an effective method for investigating species with slow metabolic rates, or for species that easily satiate. For example, allowing species to regulate an aquarium's temperature may allow more species comparisons than food reinforcers.

Based on the divergence between our individual versus group findings, we believe it is critical for temporal control researchers, behaviorists, and psychologists in general, to consider the individual subject in addition to the current trend of focusing on aggregate or group analyses. The reported bin, PRP, and IRT analyses found evidence of temporal control only when considering pooled and group responses, but not for individual subject or trial analyses. Performing individual analyses allows the researcher to focus on the real, actual observations and perform analyzes that are not taken to an abstract, aggregate level. Relying on realistic and individual data analysis methods may help cultivate a culture of designing elegantly simple protocols that do not require a hodgepodge of statistical analyses, post hoc aggregate analyses, and group designs. In moving towards more generalizable reinforcers and responses, and by eschewing potential aggregate artifacts, temporal control researchers may return a classic interest within comparative psychology to a more realistic enterprise. Considerations of the number of sessions, trials, inter-session-intervals, fixed interval durations, marking stimuli, and motivating operations are also important, but are likely easier to standardize between temporal control researchers and laboratories.

Finally, our utilization of OOM rather than traditional null hypothesis significance testing (NHST) or Bayesian methods is a major contribution to the fixed interval literature. Observation Oriented Modeling is based in a frequency paradigm and does not focus on probabilities or subjectivity (Efron, 1986); because of this, OOM is more analogous to NHST than Bayesian methods. Observation Oriented Modeling differs from NHST (in several ways, and we believe these departures comprise some of the strengths of OOM.

First, OOM does not make assumptions about homogeneity, sphericity, continuity, independence, or hypothetical distributions (e.g., normal, chi-square). The departure from relying on subjective prior or hypothetical distributions is an important factor, for not comparing the observations to a normal distribution eschews alpha-level considerations; thus, any number of assessments can be made without concerns of degrees of freedom, type I or II errors, and drawing false conclusions about a population parameter. One of the noted issues with Bayesian methods is that the researcher may inadvertently select an inappropriate representative prior distribution (Bem, Utts, & Johnson, 2011); as OOM creates its own distributions via randomization, this subjective concern is not an issue. Because alpha-levels are irrelevant within OOM, the researcher is able (and encouraged) to perform multiple analyses of the same observations using any number of a priori driven ordinal predictions. Thus, OOM facilitates the use of abduction by allowing the researcher to assess multiple hypotheses, and then identify which hypothesis best explains the observations. This is why, in several cases, we

assessed monotonic increasing and decreasing ordinal predictions. In contrast, NHST posits a single hypothesis (i.e., the null) and the rejects (which in practice accepts a second, untested hypothesis) or fails to reject a hypothesis. Null hypothesis significance testing is limited in what hypothesis can be assessed and is hypo-deductive while OOM is limited only by the number of orders that are compared.

Due to its abduction, OOM further departs from Bayesian methods which are often characterized as an inference engine (e.g., Lindley & Smith, 1972; Gelman, 2008); OOM requires a priori predictions, but the researcher must evaluate the evidence for and against each prediction before drawing conclusions; oftentimes, hundreds of ordinal assessments must be considered (e.g., Abramson, et al. 2015). The *c*-value, while similar to a *p*-value, is not the *gold standard* to determine if a hypothesis is to be rejected or supported; instead, the PCC value (more analogous to an effect size), and its relation to the randomization range, is more critical for the researcher to consider. Thus, inferences from OOM analyses are based in relativity and are not inherently subjective, and OOM is not an automatic (or universal) inference machine as Bayesian advocates appear to believe of their methods (Gigerenzer & Marewski, 2015).

Second, while NHST simply assesses if a difference between populations is observed, OOM assess the direction of the difference between observations. In this sense, OOM eschews concerns about type III errors, and asks a more complicated question than NHST. Understanding if a difference between groups exists is the first step; OOM provides methods to understand the direction of this difference. This is a notable difference between OOM and NHST, and this factor makes comparisons between these methods difficult; OOM and NHST ask fundamentally different questions.

Third, OOM remains close to the collected observations and does not make attempts to estimate population parameters that, in reality, do not exist. While NHST relies on aggregate analyses, Bayesian methods need not do so; however, Bayesian advocates often do calculate prior aggregates (e.g., Western & Jackman, 1994). Because OOM avoids aggregates and encourages individual subject analyses, outliers are easier to identify, and non-representative aggregates are not utilized to make inferences about a population parameter that not only does not represent the sample, but also does not represent the individuals that comprise the sample. This is why we justified our use of OOM for these fixed interval data, but this concern generalizes past comparative timing investigations. Animal behavior investigators were once championed as the only subfield within psychology that focused on individual subjects (Mace & Kratochwill, 1986); our use of OOM within the comparative timing literature continues this rich tradition.

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## References

- Abramson, C. I., Craig, D. P. A., Varnon, C. A., Wells, H. (2015). The effect of ethanol on reversal learning in honey bees (*Apis mellifera anatolica*): Response inhibition in a social insect model. *Alcohol*, *49*, 245-258.
- Anderson, M. C., & Shettleworth, S. J. (1977). Behavioral adaptation to fixed-interval and fixed-time food delivery in golden hamsters. *Journal of the Experimental Analysis of Behavior*, *25*, 33-49.
- Balci, F., Ludvig, E. A., & Brunner, D. (2010). Within-session modulation of timed anticipatory responding: When to start responding. *Behavioural Processes*, *85*, 204-206.
- Balci, F., Ludvig, E. A., Gibson, J. M., Allen, B. D., Frank, K. M., Kapustinski, B. J., Fedolak, T. E., & Brunner, D. (2008). Pharmacological manipulations of interval timing using the peak procedure in male C3H mice. *Psychopharmacology*, *201*, 67-80.
- Barrett, J. E. (1976). Effects of alcohol, chlordiazepoxide, cocaine and pentobarbital on responding maintained under fixed-interval schedules of food or shock presentation. *The Journal of Pharmacology and Experimental Therapeutics*, *196*, 605-615.
- Bem, D. J., Utts, J., & Johnson, W. O. (2011). Must psychologists change the way they analyze their data?. *Journal of Personality and Social Psychology*, *101*, 716-719.
- Boisvert, M. J., & Sherry, D. F. (2006). Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. *Current Biology*, *16*, 1636-1640.
- Branch, M. N., & Gollub, L. R. (1974). A detailed analysis of the effects of d-amphetamine on behavior under fixed-interval schedules. *Journal of the Experimental Analysis of Behavior*, *21*, 519-539.
- Brodbeck, D. R., Hampton, R. R., & Cheng, K. (1998). Timing behaviour of black-capped chickadees (*Parus atricapillus*). *Behavioural Processes*, *44*, 183-195.
- Byrd, L. D. (1973). Effects of d-amphetamine on schedule-controlled key presses and drinking in the chimpanzee. *The Journal of Pharmacology and Experimental Therapeutics*, *185*, 633-641.
- Byrd, L. D. (1975). Contrasting effects of morphine on schedule controlled behavior in the chimpanzee and baboon. *The Journal of Pharmacology and Experimental Therapeutics*, *193*, 861-869.
- Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules*, New York, NY: Appleton-Century-Crofts.
- Cheng, K., & Westwood, R. (1993). Analysis of single trials in pigeons' timing performance. *Journal of Experimental Psychology: Animal Behavior Processes*, *19*, 56-67.
- Cheng, K., Westwood, R., & Crystal, J. D. (1993). Memory variance in the peck procedure of timing in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *19*, 68-76.
- Church, R. M. & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 165-186.
- Church, R. M., Meck, W. H., & Gibbon, J. (1994). Application of scalar timing theory to individual trials. *Journal of Experimental Psychology: Animal Behavior Processes*, *20*, 135-155.
- Cloar, F. T., & Melvin, K. B. (1968) Performance of two species of quail on basic reinforcement schedules. *Journal of the Experimental Analysis of Behavior*, *11*, 187-190.
- Craig, D. P. A., Grice, J. W., Varnon, C. A., Gibson, B., Sokolowski, M. B. C., & Abramson, C. I. (2012). Social reinforcement delays in free-flying honey bees (*Apis mellifera* L.). *PLoS ONE*, *7*, e46729.
- Craig, D. P. A., Varnon, C. A., Sokolowski, M. B. C., Wells, H., & Abramson, C. I. (2014). An assessment of fixed interval timing in free-flying honey bees (*Apis mellifera ligustica*): An analysis of individual performance. *PLoS ONE*, *9*, e101262.
- Cumming, W. W., & Schoenfeld, W. N. (1958). Behavior under extended exposure to a high-value fixed interval reinforcement schedule. *Journal of the Experimental Analysis of Behavior*, *1*, 245-263.
- Dews, P. B. (1978). Studies on responding under fixed-interval schedules of reinforcement: II. The scalloped pattern of the cumulative record. *Journal of the Experimental Analysis of Behavior*, *29*, 67-75.

- Dinges, C. W., Avalos, A., Abramson, C. I., Craig, D. P. A., Austin, Z. M., Varnon, C. A., . . . Wells, H. (2013). Aversive conditioning in honey bees (*Apis mellifera anatolica*): A comparison of drones and workers. *The Journal of Experimental Biology*, *216*, 4124-4134.
- Dukich, T. D., & Lee, A. E. (1973). A comparison of measures of responding under fixed-interval schedules. *Journal of the Experimental Analysis of Behavior*, *20*, 281-290.
- Efron, B. (1986). Why isn't everyone a Bayesian?. *The American Statistician*, *40*, 1-5.
- Eskin, R. M., & Bitterman, M. E. (1960). Fixed-interval and fixed-ratio performance in the fish as a function of prefeeding. *The American Journal of Psychology*, *73*, 417-423.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. New York, NY: Appleton-Century-Crofts.
- Ferster, C. B., & Zimmerman, J. (1963). Fixed-interval with added stimuli in monkeys. *Journal of the Experimental Analysis of Behavior*, *6*, 317-322.
- Franck, I. (1986). Perspectives on Individual Differences. In J. Valsiner (Ed.), *The individual subject and scientific psychology*. New York, NY: Plenum.
- Gelman, A. (2008). Objections to Bayesian statistics. *Bayesian Analysis*, *3*, 445-450.
- Gentry, G. D., Weiss, B., & Laties, V. G. (1983). The microanalysis of fixed-interval responding. *Journal of the Experimental Analysis of Behavior*, *39*, 327-343.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*, 279-325.
- Gigerenzer, G., & Marewski, J. N. (2015). Surrogate science: The idol of a universal method for scientific inference. *Journal of Management*, *41*, 421-440.
- Ginsburg, N. (1960). Conditioned vocalization in the budgerigar. *Journal of Comparative Physiological Psychology*, *53*, 180-186.
- Gleitman, H., & Bernheim, J. W. (1963). Retention of fixed-interval performance in rats. *Journal of Comparative and Physiological Psychology*, *58*, 839-841.
- Gonzalez, R. C., Eskin, R. M., & Bitterman, M. E. (1962). Extinction in the fish after partial and consistent reinforcement with number of reinforcements equated. *Journal of Comparative and Physiological Psychology*, *55*, 381-386.
- Grice, J. W. (2011). *Observation Oriented Modeling: Analysis of Cause in the Behavioral Sciences*. San Diego, CA: Elsevier.
- Grice, J. W. (2014). Observation oriented modeling: Preparing students for research in the 21st century. *Innovative Teaching*, *3*, 3.
- Grossmann, K. E. (1973). Continuous, fixed-ratio, and fixed-interval reinforcement in honey bees. *Journal of the Experimental Analysis of Behavior*, *20*, 105-109.
- Guttman, N. (1953). Operant conditioning, extinction, and periodic reinforcement in relation to concentration of sucrose used as reinforcing agent. *Journal of Experimental Psychology*, *46*, 213-224.
- Haney, R. R., Bedford, J. A., & Berryman, R. (1971). Schedule control in the white-necked raven, *Corvus cryptoleucus*. *Psychonomic Science*, *23*, 104-105.
- Hanson, S. J., & Killeen, P. R. (1981). Measurement and modeling of behavior under fixed-interval schedules of reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*, 129-139.
- Herrnstein, R. J., & Morse, W. H. (1957). Effects of pentobarbital on intermittently reinforced behavior. *Science*, *125*, 929-931.
- Higa, J. J., & Simm, L. A. (2004). Interval timing in Siamese fighting fish (*Betta splendens*). *Behavioural Processes*, *67*, 501-509.
- Hoyert, M. S. (1992). Order and chaos in fixed-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, *57*, 339 - 363.
- Kleinginna, P. R., & Currie, J. A. (1979). Effects of intermittent reinforcement in the Florida kingsnake (*Lampropeltis getulus floridana*). *Journal of Biological Psychology*, *21*, 14-16.
- Laurent, E., & Lejeune, H. (1985). Temporal regulation of behavior in a fresh water turtle, *Pseudemys scripta elegans* (Wied). *Behavioural Processes*, *10*, 159-160.
- Lejeune, H. (1971). Note sur les regulations temporelles acquises en programme a intervalle fixe chez le chat. *Revue de Comportement Animal*, *5*, 123-129.
- Lejeune, H., & Richelle, M. (1982). Fixed-interval performance in turtle doves: A comparison with pigeons and rats. *Behaviour Analysis Letters*, *2*, 87-95.

- Lejeune, H., & Wearden, J. H. (1991). The comparative psychology of fixed-interval responding: Some quantitative analysis. *Learning and Motivation*, 22, 84-111.
- Lindley, D. V., & Smith, A. F. M. (1972). Bayes estimates for the linear model. *Journal of the Royal Statistical Society. Series B (Methodological)*, 34, 1-41.
- Lowe, C. F., Davey, G. C. L., & Harzem, P. (1974). Effects of reinforcement magnitude on interval and ratio schedules. *Journal of the Experimental Analysis of Behavior*, 22, 553-560.
- Lowe, C. F., & Harzem, P. (1977). Species differences in temporal control of behavior. *Journal of the Experimental Analysis of Behavior*, 28, 189-201.
- Mace, C., & Kratochwill, T. (1986). The individual subject in behavioral analysis research. In J. Valsiner (Ed.), *The individual subject and scientific psychology*. New York, NY: Plenum.
- Mechner, F., Guevrekian, L. & Mechner, V. (1963). A fixed interval schedule in which the interval is initiated by a response. *Journal of the Experimental Analysis of Behavior*, 6, 323-330.
- Michell, J. (1994). Numbers as quantitative relations and the traditional theory of measurement. *The British Society for the Philosophy of Science*, 45, 389-406.
- Michell, J. (1997). Quantitative science and the definition of measurement in psychology. *British Journal of Psychology*, 88, 355-383.
- Myers, R. D., & Mesker, D. C. (1960). Operant responding in a horse under several schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, 3, 161-164.
- Neuringer, A. J., & Schneider, B. A. (1968). Separating the effects of interreinforcement time and number of interreinforcement responses. *Journal of the Experimental Analysis of Behavior*, 11, 661-667.
- Place, A. J., Varnon, C. V., Craig, D. P. A., Abramson C. I. (in press). Exploratory investigations in operant thermoregulation in rattlesnakes (*Crotalus atrox* and *Crotalus horridus*). In W. K. Hayes, K. R. Beaman, M. D. Cardwell, S. P. Bush (Eds.), *The Biology of Rattlesnakes II*. Loma Linda, CA: Loma Linda University Press.
- Powell, R. W. (1972). Responding under basic schedules of reinforcement in the crow. *Journal of Comparative and Physiological Psychology*, 79, 156-164.
- Rakitin, B.C., Gibbon, J., Penney, T. B., Malapani, C., Hinton, S. C., & Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 24, 15-33.
- Richelle, M., & Lejeune, H. (1980). *Time in animal behavior*. Oxford, England: Pergamon Press.
- Richelle, M., & Lejeune, H. (1984). Timing competence and timing performance: A cross-species approach. *Annals of the New York Academy of Sciences*, 423, 254-268.
- Rozin, P. (1965). Temperature independence of an arbitrary temporal discrimination in the goldfish. *Science*, 149, 561-563.
- Rubin, H. B., & Brown H. J. (1969) The rabbit as a subject in behavioral research. *Journal of the Experimental Analysis of Behavior*, 12, 663-667.
- Schneider, B. A. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior*, 12, 677-687.
- Shull, R. L. (1970). A response-initiated fixed-interval schedule of reinforcement. *Journal of the Experimental Analysis of Behavior*, 13, 13-15.
- Skinner, B. F. (1938). *The behavior of organisms*. New York, NY: Appleton-Century-Crofts.
- Sokolowski M. B., & Abramson C. I. (2010). From foraging to operant conditioning: A new computer-controlled Skinner box to study free-flying nectar gathering behavior in bees. *Journal of Neuroscience Methods*, 188, 235-242.
- Stevens, S. S. (1946). On the theory of scales of measurement. *Science*, 103, 677-680.
- Stubbs, D. A. (1976). Scaling of stimulus duration by pigeons. *Journal of the Experimental Analysis of Behavior*, 26, 15-25.
- Taylor, P. E., Haskell, M., Appleby, M. C., & Waran, N. K. (2002). Perception of time duration by domestic hens. *Applied Animal Behaviour Science*, 76, 41-51.
- Todd, G. E., & Cogan, D. C. (1978). Selected schedules of reinforcement in the black-tailed prairie dog (*Cynomys ludovicianus*). *Animal Learning & Behavior*, 6, 429-434.
- Toelch, U., & Winter, Y. (2013). Interval timing behavior in Pallas's long-tongued bat (*Glossophaga soricina*). *Journal of Comparative Psychology*, 127, 445-452.
- Vander Weele, D. A., & Abelson, R. M. (1973). Selected schedules of reinforcement in the Mongolian gerbil. *Psychological Reports*, 33, 99-104.

- Waller, B. (1961). Effects of chronically administered chlorpromazine on multiple-schedule performance. *Journal of the Experimental Analysis of Behavior*, 4, 351-359.
- Weiss, B., & Moore, E. W. (1956). Drive level as a factor in distribution of responses in fixed-interval reinforcement. *Journal of Experimental Psychology*, 52, 82-84.
- Wenger, G. R., & Dews, P. B. (1976). The effects of phencyclidine, ketamine, d-amphetamine and pentobarbital on schedule-controlled behavior in the mouse. *The Journal of Pharmacology and Experimental Therapeutics*, 196, 616-624.
- Western, B., & Jackman, S. (1994). Bayesian inference for comparative research. *American Political Science Review*, 88, 412-423.
- Zeiler, M. D., & Powell, D. G. (1994). Temporal control in fixed-interval schedules. *Journal of the Experimental Analysis of Behavior*, 61, 1-9.

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