

## Evolution and Relationships: The Integration Continues

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In this commentary, I highlight the importance of conceptualizing research at the interface of evolution and relationships within Tinbergen's (1963) different levels of explanation. In doing so, I also discuss how each of the target articles in this special issue fit within these levels, and clarify why novel information associated with each level can, at times, provide unique insights into a given trait or behavior that yields significantly deeper understanding. I then overview 3 recent theoretical papers that integrate principles and findings across evolution and relationship science: love as a commitment device (Fletcher, Simpson, Campbell, & Overall, 2015), functional interdependence theory (Balliet, Tybur, & Van Lange, 2016), and the conflict-confluence model (Durante, Eastwick, Finkel, Gangestad, & Simpson, 2016). Each of these new theories/models generates many novel, specific predictions that provide excellent roadmaps for future investigators. Viewed as a whole, the target articles and commentaries that comprise this special issue reveal many of the theoretical and empirical gains that have been made in recent years.

*Keywords:* evolution, relationships, theoretical models

The first special issue devoted to evolution and interpersonal relationships appeared in *Personal Relationships* in 2001. At that time, the field of evolutionary psychology was relatively young, but its theoretical power and promise were evident. The field of relationship science was becoming more prominent within several social and behavioral science disciplines, but many of its empirical findings were not well-integrated with major life span theories and models. The goal of that special issue was to introduce evolutionary theories and thinking to relationship scholars and, at the same time, to introduce the rich empirical terrain of relationship science to evolutionary scholars (see Simpson & Gangestad, 2001). We believed that the science of relationships could benefit from an infusion of evolutionary thinking, and that evolutionary psychologists could benefit from exposure to the rapidly growing body of findings that anchored relationship science.

This special issue provides a glimpse of how that goal has borne out. Some of the cross-fertilization we had hoped for has occurred. More evolutionary psychologists are applying their arsenal of theories to clarify and deepen our understanding of various relationship dynamics, processes, and outcomes (see, e.g., the articles by French and colleagues, Meltzer, and Szepeswöl and colleagues in this special issue). Moreover, a growing number of relationships scholars are examining many important relationship phenomena through the lens of evolutionary theories and models (see the articles by Chang and colleagues, Cooper and colleagues, and Wright). This is encouraging because both fields have a great deal to offer one another. The integration, however, must continue. In this commentary, I discuss several prominent themes, recent trends, and future directions that could further facilitate this process.

### Levels of Explanation

One of the most important articles in the history of the life sciences was published by the famous ethologist, Niko Tinbergen, in 1963. Partly in response to a series of heated debates

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about whether nature or nurture was more important in shaping the development and behavior of organisms, Tinbergen pointed out that questions of the form “Why does organism A possess trait X and/or engage in behavior Y?” must be considered at four levels of explanation, and scholars from different disciplines commonly seek answers to questions framed at different levels.

Questions dealing with *proximate causation*, which relationship scholars typically address, focus on how factors within a person’s immediate environment activate, maintain, and regulate a given trait or behavior. For example, what specific features of each relationship partner (or their joint attributes) promote stronger and more lasting pair-bonds? Questions addressing *ontogeny*, on which developmental scholars frequently focus, address how a trait or behavior emerges and changes as a person develops across the life-course. How, for example, do children learn certain skills or values that predict involvement in stronger pair-bonded romantic relationships later in life? Questions of *phylogeny*, which often are of interest to comparative psychologists, examine the ancestral origins of a specific trait or behavior in relation to other species on the phylogenetic tree. When and how, for instance, has pair-bonding evolved in other species during evolutionary history, and how does this knowledge affect our understanding of pair-bonding in humans? Questions of *ultimate causation*, which tend to be of focal interest to evolutionary psychologists, center on the selection pressures that may have produced a given trait or behavior. What, for example, were the specific selection forces in ancestral environments that shaped pair-bonding and serial monogamy in humans?

Each level of explanation can clarify and extend our understanding of a trait or behavior in unique ways (Eastwick, 2009). Consider a well-known finding in relationship science. In most contexts, propinquity, similarity, and frequency of contact are powerful predictors of romantic attraction (Clark & Lemay, 2010). One glaring exception to this rule is when opposite-sex individuals are raised in the same home, similar to siblings (Lieberman, Tooby, & Cosmides, 2007). When biologically unrelated children are reared together, they almost never become romantically involved as adults (van den Berghe, 1983). In a famous study of ap-

proximately 3,000 kibbutz marriages in Israel (Shepher, 1971), children raised from birth in the same household units never married each other, even though such marriages were permitted and individuals often married others raised in nearby units. This striking violation of the general attraction rule is understandable, but only when viewed from an ultimate level of explanation. Given the negative consequences of inbreeding, humans should have evolved propensities (psychological mechanisms) that inhibited romantic attraction to same-age persons with whom they were raised and, therefore, could be biologically related. Each level of explanation of incest avoidance—why it exists (ultimate causation), how it develops (ontogeny), and what cues activate and terminate its expression (proximate causation)—provides novel and important information that other levels do not.

Only two levels of explanation—ontogenetic and proximate—are psychological in nature. Why, then, should ultimate-level questions be relevant to scholars interested in understanding specific psychological processes and outcomes? One answer is that questions dealing with ultimate explanation—questions about the functional design or purpose of a given trait or behavior—can inform how and why proximate mechanisms operate the way they do. Consider another example—research on ovulatory shift effects in women within the context of romantic relationships.

According to sexual selection theory (Trivers, 1972) and the strategic pluralism model (Gangestad & Simpson, 2000), there should be contexts in which women—even those involved in committed, long-term relationships—should be attracted to men who possess honest markers (traits or behaviors) of “good genes.” These markers, however, should be most attractive to women when the genetic benefits of such men can be obtained, such as when women can conceive during their monthly reproductive cycle. Indeed, a substantial body of research indicates that heterosexual women are more attracted to men who display certain “good genes” markers, but only when they are ovulating and evaluating these men as potential short-term mates (see Gildersleeve, Haselton, & Fales, 2014, for a meta-analytic review). This unique, specific, and nonintuitive finding was anticipated by evolutionary theories. It was not

anticipated a priori by other nonevolutionary theories of human mating.

### The Current Articles

Each of the articles in this special issue address one or more of Tinbergen's (1963) four levels of explanation, focusing on different romantic relationship processes and outcomes. Most of the articles directly apply evolutionary thinking to frame hypotheses that focus on processes and/or outcomes at the proximate or ontogenetic level.

Two articles utilize evolutionary principles to derive predictions about how women and men should behave across the female partner's reproductive cycle. Borrowing principles from sexual selection theory (Trivers, 1972), the strategic pluralism model (Gangestad & Simpson, 2000), and evolutionary-based ideas associated with ovulatory shifts (e.g., Gangestad, Thornhill, & Garver-Apgar, 2005), Meltzer (2017) investigates how a male partner's degree of masculinity is related to his partner's (wife's) marital satisfaction when she is versus is not ovulating. Meltzer finds that conception risk (ovulation) is positively associated with marital satisfaction in normally cycling wives whose husbands report being more masculine. Conception risk, however, is not associated with marital satisfaction among normally cycling wives with less masculine husbands. Consistent with prior work on ovulatory shifts (e.g., Gangestad et al., 2005), these results indicate that women's conception status interacts with a specific marker of their partners' "good genes" (masculinity) to affect women's level of relationship satisfaction. This finding is important because it reveals how attraction patterns are systematically tied to another marker of good genes in men, even in long-term, presumably pair-bonded relationships.

Melding principles from models of evolved sex differences in mating and jealousy (e.g., Buss, 2000; Daly, Wilson, & Weghorst, 1982), French and colleagues (2017) examine the role that hormonal contraceptives (HCs) play in perceptions of commitment and mate-guarding behavior in men over their female partner's reproductive cycle. They find that newlywed husbands who perceive that their wives are less committed tend to engage in more mate-guarding behavior. This association, however, is contingent on their wives' use of HCs. Among husbands whose wives were

not using HCs, less perceived partner commitment predicted more husband mate-guarding. But among husbands whose wives were using HCs, husbands' perceived partner commitment was not related to their amount of mate-guarding. These novel findings suggest that HCs, which are commonly used in long-term relationships, may disrupt important evolved relationship processes. This is important information, especially for couples in which women are coming off of HCs.

Using principles from life span evolutionary models of social development (e.g., Belsky, Steinberg, & Draper, 1991) to address questions of ontogeny, Szepeswol and colleagues (2017) test how specific early life experiences lead individuals to adopt either restricted/longer-term or unrestricted/shorter-term mating orientations in early adulthood. They show that experiencing more predictable environments during the first 4 years of life prospectively predicts restricted sociosexuality at Age 23, which is serially mediated by more maternal support early in life and having more secure representations of childhood at Age 19. This is the first prospective study to document the early life origins of restricted and unrestricted mating orientations, including one of the theoretically anticipated mediating pathways.

Merging principles from sexual selection theory (Trivers, 1972), the strategic pluralism model (Gangestad & Simpson, 2000), and evolutionary models of parental investment (e.g., Geary, 2000), Chang and colleagues (2017) test predictions about parental investment in relation to each partner's perceived mate value. They find that men who perceive having higher levels of "good genes" and good-provider mate attributes (relative to the mate attributes of their female partners) report providing less parental investment in their children compared with men with lower levels of these mate attributes. These findings reveal a theoretically anticipated gender-based conflict of interest in heterosexual relationships by suggesting that the evolution of good-father and good-mother mate preferences may be meaningfully tied to the different ways in which males and females reproduce.

Two articles in the special issue infuse evolutionary thinking more indirectly by investigating the role of adult romantic attachment orientations (styles) in predicting intimate partner aggression and daily relationship quality. Several evolutionary scholars (e.g., Belsky et al.,

1991; Kirkpatrick, 1998) have proposed that secure and insecure romantic attachment orientations, which stem, in part, from how individuals have been treated by prior attachment figures, reflect different mating strategies. Securely attached individuals, who have received more and better care/support from past attachment figures, typically adopt a slower, more restricted mating strategy, whereas insecurely attached individuals (both anxious and avoidant), who have received less and poorer care/support, usually adopt a faster, more unrestricted mating strategy (see Simpson & Belsky, 2016, for a review).

Wright (2017) investigates whether insecurely attached individuals are more inclined to engage in intimate partner aggression and whether this association is mediated by variables such as jealousy or anger. She finds that the level of jealousy does, in fact, mediate this connection, and that similar patterns exist for anger, privacy invasion, and cyber/tech privacy invasion. These findings are noteworthy because they identify some of the specific psychological states that may translate attachment insecurity into aggressive behavior in long-term romantic relationships.

Cooper and colleagues (2017) explore how attachment orientations along with approach and avoidance sacrifice motives covary with daily relationship quality in same-sex romantic couples. They find a positive association between approach motives and daily relationship quality, but a negative one between avoidance motives and daily quality. These effects, however, are moderated by both attachment orientations and gender. Specifically, although stronger approach motives predict higher relationship quality, and stronger avoidance motives predict lower relationship quality, this is especially true for more securely attached women and for more insecurely attached men. These findings highlight the importance of recognizing the intricate ties between approach and avoidance sacrifice motives, secure and insecure attachment orientations, and gender when predicting daily relationship quality, particularly among people involved in same-sex romantic relationships.

### Future Directions

The articles in this special issue showcase just some of the good empirical work being

done at the intersection of evolution and relationships. There also have been some promising theoretical extensions and advances in the past couple of years, three of which are highlighted below. All three of these extensions/advances provide good roadmaps for where research at the intersection of evolution and relationships can and perhaps should head in the next decade.

### Love as a Commitment Device

Consistent with the special issue's theme of long-term committed relationships, there now is fairly compelling evidence that love is an evolved commitment device (Frank, 1988) designed to keep mates pair-bonded long enough to facilitate the growth and development of their offspring. Fletcher, Simpson, Campbell, and Overall (2015) review considerable evidence that pair-bonding, which is promoted by feeling love for one's mate, helped our ancestors provide the huge amount of biparental care and investment needed to rear and socialize children to reproductive age. Fletcher et al. (2015) also suggest that managing long-term pair-bonds and other family relationships facilitated the evolution of greater social intelligence and more extensive cooperation, both of which are unique features of humans. These theoretical propositions are supported by a wide array of findings from many disciplines in the social, behavioral, and life sciences. For example, consistent with the premise that romantic love is an evolved commitment device that facilitated pair-bonding, Fletcher and colleagues review evidence indicating that (a) love is universal (i.e., it is experienced in virtually every current and past culture); (b) it suppresses mate-search desires and associated psychological mechanisms; (c) it has specific and unique behavioral, hormonal, and neuropsychological patterns; and (d) it predicts better long-term health and survival rates.

This does imply that everyone experiences love and pair-bonding in the same way or at the same pace as relationships develop. Humans also evolved to be serially monogamous (Fisher, 1992). Moreover, there is considerable variability within men and women in the enactment of slow/restricted versus fast/unrestricted mating strategies (Gangestad & Simpson, 2000) and in the desire for long-term versus short-term relationships (Buss & Schmitt, 1993). We still do not know whether people who adopt a fast/unrestricted strategy or desire short-term rela-

tionships experience love and pair-bonding differently than people who are slow/restricted or want long-term relationships, but important theoretical and empirical work is beginning to be conducted on this topic (see Eastwick, 2016).

There also needs to be more work *directly* integrating major relationship theories, models, and principles with major evolutionary ones. Some good, integrative theoretical work has already taken place with respect to attachment theory (e.g., Belsky et al., 1991; Del Giudice, 2009; Kirkpatrick, 1998), which makes sense given that attachment theory is a middle-level evolutionary theory (Bowlby, 1969; Simpson, 1999). Two recent examples of further integration efforts are theoretical articles by Balliet, Tybur, and Van Lange (2016) and by Durante, Eastwick, Finkel, Gangestad, and Simpson (2016), both of which are discussed below.

### Functional Interdependence Theory

In an attempt to bridge evolutionary psychology (Buss, 1995; Tooby & Cosmides, 1992) and interdependence theory (Kelley, 2003; Kelley & Thibaut, 1978), Balliet et al. (2016) developed a model termed *functional interdependence theory* (FIT). The model has three core propositions. First, four forms (types) of interdependence most likely characterized many social interactions in our ancestral past. They include (a) the degree of interdependence (i.e., the extent to which relationship partners must rely on each other to accomplish an important plan or goal in a given situation), (b) the degree of correspondence (i.e., the extent to which each partner's best outcome in a given situation is similar vs. different), (c) the basis for interdependence (i.e., the extent to which an individual can influence how his or her partner affects the individual's outcomes in a given situation), and (d) the amount of asymmetric dependence (i.e., the extent to which an individual is unilaterally dependent on his or her partner in a given situation). Each form of interdependence should have generated specific psychological adaptations (psychological mechanisms) that helped our ancestors estimate both the form and amount of interdependence they had with a particular person in a specific social context.

Second, being able to accurately infer and respond to the form of interdependence in a given situation should have allowed individuals to understand and influence other people more effec-

tively, choose better or more appropriate partners for specific tasks, and notice and adjust to changing patterns of interdependence as social contexts changed. Third, these evolved psychological adaptations should have helped individuals estimate, monitor, and manage different forms of interdependence with different partners by improving individuals' ability to integrate, track, and store relevant information in memory.

The FIT makes several unique, testable predictions about the conditions under which individuals should initiate and maintain cooperative relationships with certain people, how and why they should choose partners for different kinds of relationships (e.g., friendships, coalitions, work relationships, romantic relationships), and when they should display certain social motives toward others (see Balliet et al., 2016). These predictions can and should be tested in the coming decade. Consider one example: food sharing. Most evolutionary models assume a single, fixed pattern of interdependence with other people that remains relatively constant across a person's life. Under this general assumption, the tit-for-tat strategy (in which an individual continues to share food as long as his or her partner reciprocates in return over time) is the best and most stable interaction strategy (Axelrod, 1984). However, most individuals have different forms of interdependence with different partners with whom food may occasionally be shared, not only today but throughout evolutionary history as well. A tit-for-tat food sharing strategy works well with peers who have similar needs, skills, and communal values; it does not work well if one's interaction partner is a child, an unskilled or poorly motivated partner, or someone who is self-centered and untrustworthy. Thus, the best strategy to adopt should depend on the degree to which an individual is interdependent on and correspondent with a specific food-sharing partner. It may also depend on the reasons why two partners are interdependent and the extent to which asymmetric dependence (power differences) characterize their relationship. When variation on these dimensions is modeled, other interaction strategies outperform tit-for-tat (see, e.g., Fischer et al., 2013). Evolutionary and relationship researchers should use the FIT as a springboard for generating and testing new hypotheses that pertain to different types of social contexts and close relationships, beyond just romantic ones.

### Conflict-Confluence Model

Another recent integrative theoretical approach has been developed by [Durante and colleagues \(2016\)](#). For decades, both relationship researchers and evolutionary psychologists have studied human mating. Some of the research generated by these two perspectives has yielded different and, at times, what appear to be contradictory findings. Research in relationship science, for example, has documented ways in which committed relationship partners seem to be motivated to maintain their current relationships (e.g., by cognitively derogating attractive alternatives), whereas research in the evolutionary sciences has focused on how individuals are often motivated to pursue their own reproductive interests, sometimes at a cost to their current partner (e.g., by having sex with attractive alternatives). Rather than being incompatible, however, these frameworks actually have different assumptions that occasionally generate contrasting predictions, leading researchers to study the same behavior in different ways.

[Durante and colleagues \(2016\)](#) have proposed a theoretical framework that attempts to reconcile some of these conflicting findings and guide future research at the intersection of evolution and relationships. This framework, known as the conflict-confluence model, views evolutionary and relationship science perspectives as existing along a continuum that reflects the extent to which mating partners' interests tend to be aligned versus misaligned. Evolutionary perspectives tend to view romantic partners as having more misaligned, competing, and conflicting interests, which motivates each partner to remain open to alternative options and look out for their own best self-interest. This, in turn, leads relationship partners to experience less correspondent outcomes, have more antagonistic interactions, and be involved in less stable relationships (see, e.g., [Buss, 1989](#); [Goetz & Shackelford, 2009](#); [Haselton, Buss, Oubaid, & Angleitner, 2005](#)). Relationships perspectives, on the other hand, typically construe romantic partners as having more aligned and confluent interests, which motivates each partner to disregard or downplay alternatives and focus on what is best for their partner and/or relationship. These tendencies result in more correspondent outcomes, more cooperative interactions, and often more stable long-term relationships (see,

e.g., [Bowlby, 1969](#); [Feeney & Collins, 2015](#); [Hazan & Shaver, 1994](#)).

The utility of the conflict-confluence model becomes evident when one examines the rather inconsistent findings on ovulatory shift effects in women, which accentuate the tension between the desire to maintain or strengthen an existing pair-bond versus the desire to seek extrapair mates. When strong conflicts of interest exist between relationship partners, individuals should be more inclined to act on their own self-interests and, as a result, their relationships should become less stable and more acrimonious. But when strong confluences of interest exist between relationship partners, individuals should behave on what is best for the relationship, resulting in more stable and content relationships.

In relation to the FIT, the conflict-confluence model suggests that relationships with stronger conflicts of interest (compared with stronger confluence of interests) should have patterns of interdependence in which the amount of interdependence and correspondence are generally low. [Durante and colleagues \(2016\)](#) discuss how specific characteristics of each partner, their relationship, the local environment, and the alternatives each partner has to the relationship ought to affect each partner's degree of conflict versus confluence of interests. The many predictions they enumerate need to be tested. For example, we need to know whether individuals who have invested a lot in their relationship share a strong bond with their partner, have fewer viable alternatives, and/or live in an environment in which biparental care is required to raise children actually have more confluence of interests, and whether individuals with the opposite set of characteristics actually experience greater conflicts of interest, on average.

### Conclusions

All of the articles in this special issue focus on romantic relationships or early experiences that shape adult mating strategies, tactics, perceptions, or behaviors. This is not surprising given the critical role that reproduction—and especially differential reproductive fitness—assumed in our evolutionary past. Evolutionary principles and thinking, however, apply well beyond romantic relationships. The evolved psychological and biological systems that generate feelings of love, which cement adult pair-bonds, most likely originated from the systems designed to ensure that

parents feel love for, and are thus motivated to remain in close contact with, their infants (Zeifman & Hazan, 2016). Moreover, both functional interdependence theory and the conflict-confluence model are applicable to different types of relationships that also affected the survival and reproductive fitness of our ancestors, including ties between friends, coalition partners, parents and their offspring, siblings, and extended family members. Future theory and research at the crossroads of evolution and relationships needs to venture beyond romantic dyads to clarify and extend our understanding of how these other crucial relationships function.

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Received March 3, 2017

Accepted March 3, 2017 ■